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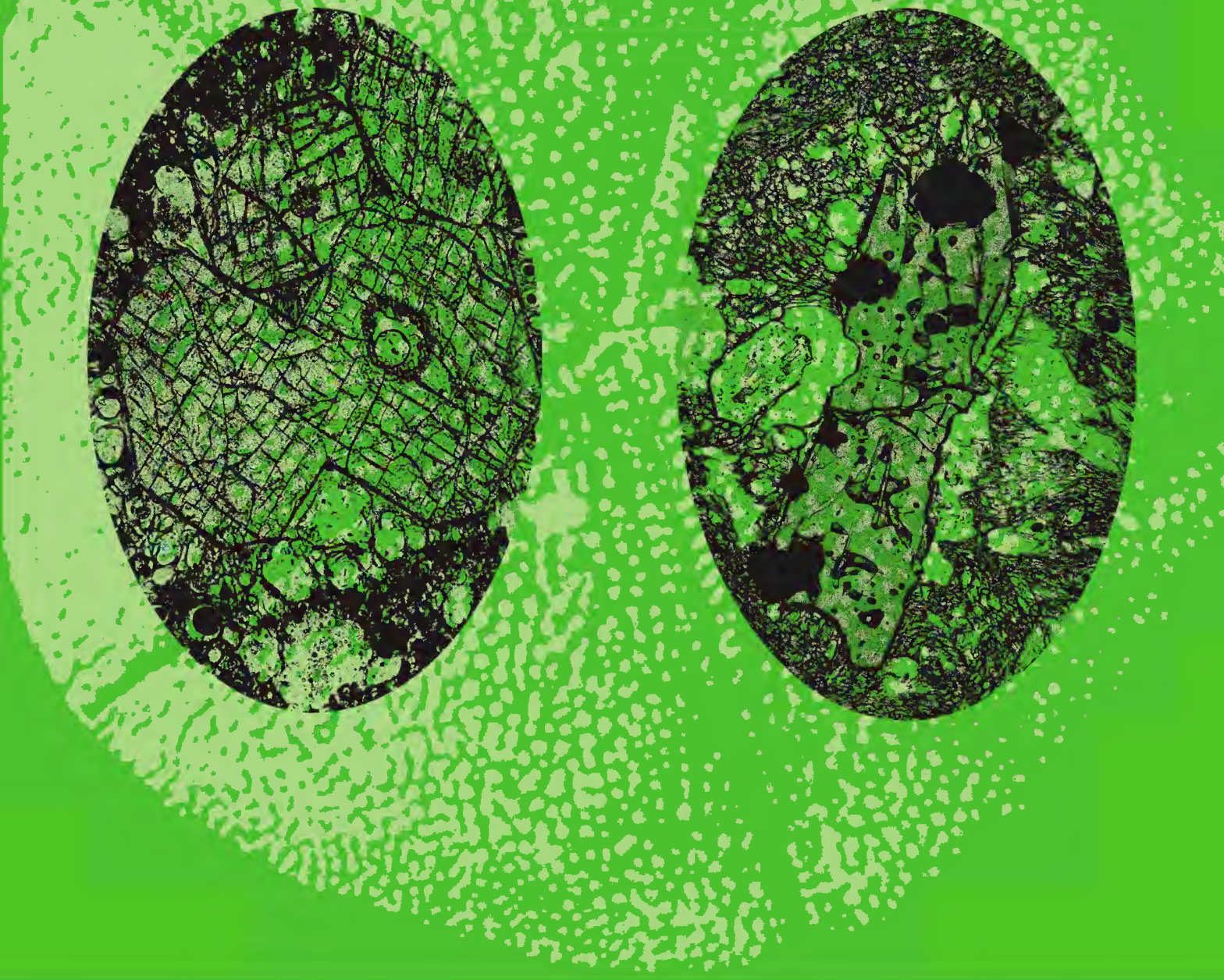
RECORDS OF THE AUSTRALIAN MUSEUM



VOLUME 58 NUMBER 2 14 June 2006

RECORDS OF THE AUSTRALIAN MUSEUM

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The **cover illustration** shows detail of form and decoration of arrows from the Highlands of Papua New Guinea. The drawings, by anthropologist Thelma Bush, were published in her 1985 paper in *Records of the Australian Museum.* The entire work may be read online at the Australian Museum Scientific Publications website:

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The background image is the actinal view of the echinoderm *Asterodiscides elegans belli,* the specimen was collected by Thurston in Madras, India, in 1890, for the British Museum, and subsequently donated to the Australian Museum. Museum malacologist, F.W.E. Rowe, revised the taxonomy of the genus in a 1977 *Records of the Australian Museum* publication and determined this specimen to be representative of a separate subspecies that he named *belli*; Birtles reported the presence of this subspecies in waters off northeastern Australia.

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A New Genus, *Warlucephala*, for the Reception of *Deltocephalus arunda* Jacobi, 1909, and Two New Species (Hemiptera: Cicadellidae: Deltocephalinae)

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ABSTRACT. The new leafhopper genus *Warlucephala* is described based on *Deltocephalus arunda* Jacobi, 1909, from Western Australia and placed in the tribe Deltocephalini. *Warlucephala reversa* n.sp. from New South Wales and *Warlucephala abbreviata* n.sp. from southern Western Australia are also described. The affinities of the new genus are discussed.

FLETCHER, M.J., 2006. A new genus, *Warlucephala*, for the reception of *Deltocephalus arunda* Jacobi, 1909, and two new species (Hemiptera: Cicadellidae: Deltocephalinae). *Records of the Australian Museum* 58(2): 125–128.

In his catalogue of the Australian leafhopper fauna, Evans (1966) listed 15 species of subfamily Deltocephalinae in the nominal genus *Deltocephalus* Burmeister but stated that a critical study of the world fauna was needed to determine if any of these were truly congeneric with the type species, *Deltocephalus pulicaris* Fallén. By 1994, when the next catalogue of the Australian fauna was published (Day & Fletcher, 1994), four of these had been transferred elsewhere: *D. taedius* Kirkaldy to *Arawa* Knight (Tribe Athysanini) as a *nomen dubium*, by Fletcher & Condello (1993), *D. montanus* Evans (preoccupied by *Deltocephalus montanus* Distant, replaced with *D. novellus* by Metcalf, 1968) to *Arawa* by Knight (1975), *D. dedarensis* Evans to *Euleimonios* Kirkaldy (Tribe Paralimnini) by Fletcher & Condello (1994) and *D. dorsalis* Motschulsky to *Recilia* Edwards (Tribe Deltocephalini) by Nielson (1968). In addition, Day & Fletcher (1994) transferred *Deltocephalus pullatus* Evans to *Limotettix* J. Sahlberg (tribe Athysanini) as a senior synonym of *Limotettix condylus* Knight.

Of the remaining 10 species listed in *Deltocephalus* by Day & Fletcher (1994), six were moved into other genera by Fletcher (2004), *D. lotis* Kirkaldy, *D. aristarche* (Kirkaldy) and *D. perparvus* Kirkaldy to *Horouta* Knight (Tribe Deltocephalini), *D. polemon* Kirkaldy to *Micrelloides* Evans (Tribe Paralimnini) and *D. decoloratus* Evans and *D. centralis* Evans to *Arawa*.

In this paper, one of the remaining four species is transferred to *Warlucephalus* n.gen. and two additional new species are added to the genus. This leaves *D. chlorippe* (Kirkaldy), *D. lucindae* Kirkaldy and *D. viridellus* Evans still to be placed outside *Deltocephalus* should this prove necessary.

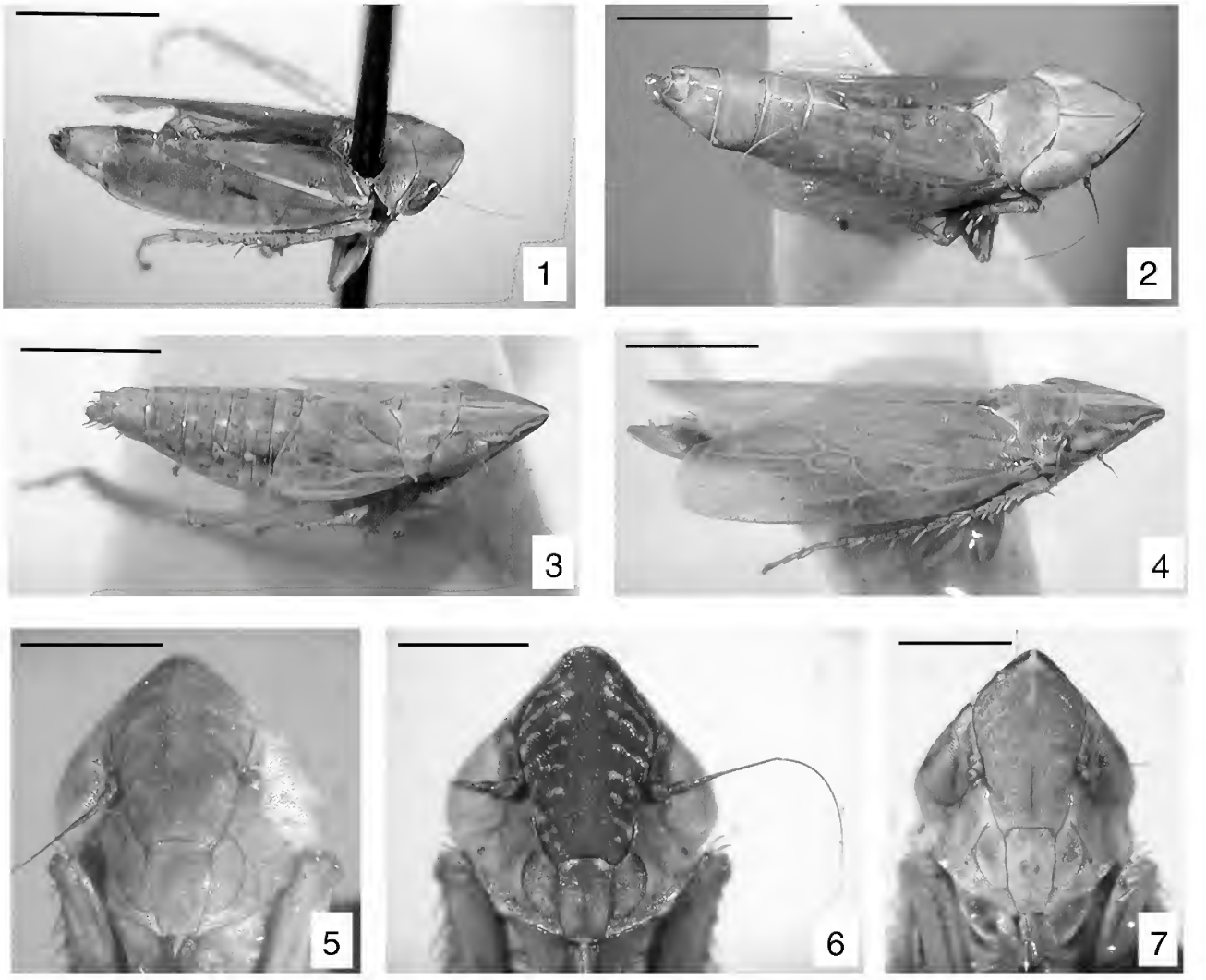
The following abbreviations are used in this paper: AM: Australian Museum, Sydney; ASCU: Agricultural Scientific Collections Unit, NSW Department of Primary Industries, Orange; NSW: New South Wales; WA: Western Australia.

Genus *Warlucephala* n.gen.

Type species. *Deltocephalus arunda* Jacobi 1909: 343.

Etymology. The generic name, which is feminine, combines flat plain (*warlu*: Nyungar language of northwestern Australia) (Thieburger & McGregor, 1994) with head (*cephalus*, Latin).

Diagnosis. *Head.* Head flat dorsally, convex on face with frontoclypeus large, anteclypeus parallel-sided or tapered to level with lora, then narrowed to apex. Vertex arrow-shaped with longitudinal median furrow around distinct coronal suture which extends from base to around three



Figs. 1–7. Habitus of (*1*) *Warlucephala arunda*, lectotype female; (*2*) *W. reversa*, paratype male; (*3*) *W. abbreviata*, holotype male; and (*4*) *W. abbreviata*, macropterous female paratype; scale lines = 1 mm. Facial views of heads of (*5*) *Warlucephala arunda*; (*6*) *W. reversa*; and (*7*) *W. abbreviata*; scale lines = 0.5 mm.

quarters length of vertex. Vertex meeting face at acute angle, sometimes marginally carinate over median section. *Tegmina*. Tegmina fully brachypterous, semi-brachypterous or macropterous. *Male genitalia*. Pygofer extended posteriorly as rounded lobe bearing macrosetae. Subgenital plates narrow triangular to elongate, bearing row of macrosetae on outer margins. Parameres modified with apical process rounded, not pointed. Aedeagus simple tubular, without processes other than apical extension of various form beyond gonopore.

Distribution. Southern Western Australia and New South Wales.

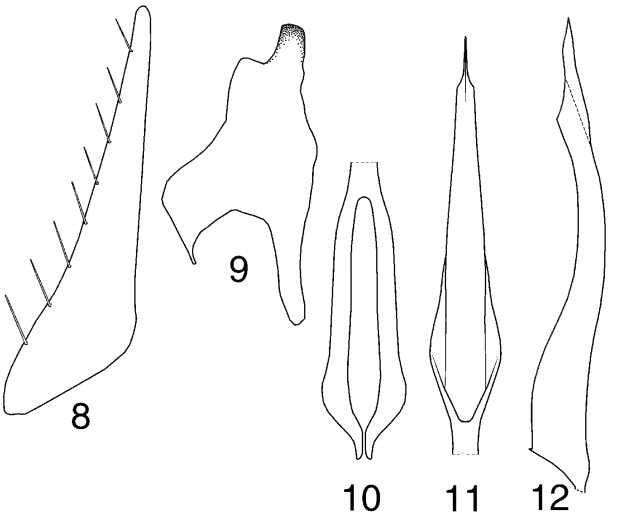
Warlucephala arunda (Jacobi), n.comb.

Figs. 1, 5, 8–12

Deltocephalus arunda Jacobi 1909: 343.

Types. Lectotype ♀ (here designated), Moora, Western Australia 8.viii.1905 (Berlin); paralectotype, ♀, same data as lectotype (?Hamburg).

Material examined. Lectotype and the following: Western Australia: 3 ♂♂, Perth, ii.1961, light trap (AM).



Figs. 8–12. Male genitalia of *Warlucephala arunda*: (*8*) subgenital plate; (*9*) paramere; (*10*) connective; (*11*) aedeagus, posteroventral view; (*12*) aedeagus, lateral view.

Description. *Length*: Male 2.8–2.9 mm. *Coloration*: Pale yellow brown on vertex, thorax and abdomen. Face (Fig. 5) dark brown with transverse pale striations on frontoclypeus, separated from vertex by two transverse dark brown lines which are slightly convex around dorsal edge of frontoclypeus. Tegmina translucent brown, paler along costal margin. *Morphology*: Anteclypeus broad at base, tapering unevenly towards apex, noticeably narrowing beyond lora which are widely separated from face margin. Vertex arrow-shaped, flat to concave on disc with clearly distinct median carina reaching three quarters from base to apex. Pronotum short. Tegmen reaching to just short of base of tenth abdominal tergite, appendix absent. *Male genitalia*: Pygofer extended posteriorly and apically rounded, bearing group of macrosetae on posterior lobe. Subgenital plates (Fig. 8) narrowly triangular, posteriorly extended to level with pygofer, apically bluntly pointed, each bearing 6–8 macrosetae evenly spaced along outer margin which is slightly concave. Paramere (Fig. 9) short, apical process reduced, bluntly rounded apically, preapical shoulder rounded. Connective (Fig. 10) fused with base of aedeagus, with lateral arms longer than main body. Aedeagus (Figs. 11–12) tubular, lightly evenly curved dorsally with gonopore apical but with shaft extended to form short, straight, linear process directed posteriorly from ventral margin of gonopore.

Distribution. Western Australia.

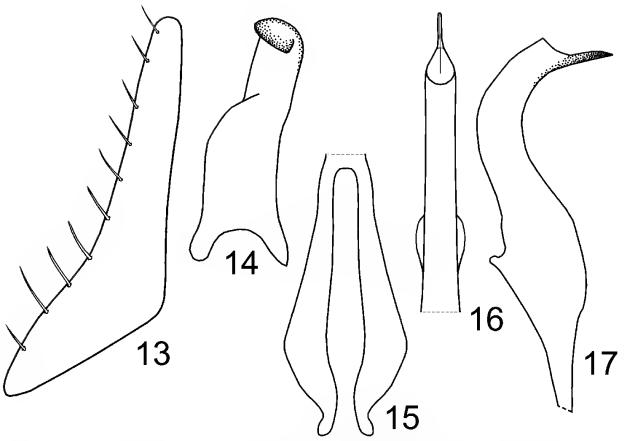
Remarks. The presence of a paralectotype female in Hamburg has not been confirmed. A lectotype is designated to provide a reference for the species. The three males listed above were found in the J.W. Evans Collection and appear to have been collected by Evans, because the associated data labels appear to be in his handwriting.

Warlucephala reversa n.sp.

Figs. 2, 6, 13–17

Type material. HOLOTYPE ♂, Mt Kosciusko [sic], Wilson's Valley, NSW, i.1965, J.W. & F. Evans, AM K204207. PARATYPES: New South Wales: 2 ♂♂, 1♀, 1 unknown (lacking abdomen), same data as holotype (1♂, 1 unknown ASCU, others AM K204208, AM K204209).

Description. *Length*. Male (n=3) 3.5–3.7 mm, female (n=1) 4.3 mm. *Coloration*: Pale brown dorsally, darker ventrally. Frontoclypeus (Fig. 6) dark brown with speckled lateral pale striations. Apex of head with fine dark brown marginal line, slightly convex dorsally around margin of frontoclypeus. Tegmina translucent testaceous with pale band along costal margin. *Morphology*: Anteclypeus parallel-sided to apex of lora, then narrowed to apex. Lora widely separated from face margin. Vertex arrow-shaped, slightly longer medially than wide between eyes. Vertex shagreen, flat, medially slightly depressed with dark median suture reaching about 3 quarters length from base. Pronotum short, faintly transversely wrinkled. *Male genitalia*. Pygofer long, laterally extended to form rounded lobe bearing 8–9 long macrosetae. Subgenital plates (Fig. 13) elongate triangular, apically roundly pointed, bearing evenly spaced macrosetae on outer, slightly concave, margins. Paramere (Fig. 14) short, with apical process rounded and curled over apically. Preapical shoulder weakly rounded. Connective (Fig. 15) with arms longer than main body. Aedeagus (Figs. 16, 17) tubular, strongly curved ventrally with apical linear extension beyond gonopore on ventral side of gonopore.



Figs. 13–17. Male genitalia of *Warlucephala reversa*: (*13*) subgenital plate; (*14*) paramere; (*15*) connective; (*16*) aedeagus, posteroventral view; (*17*) aedeagus, lateral view.

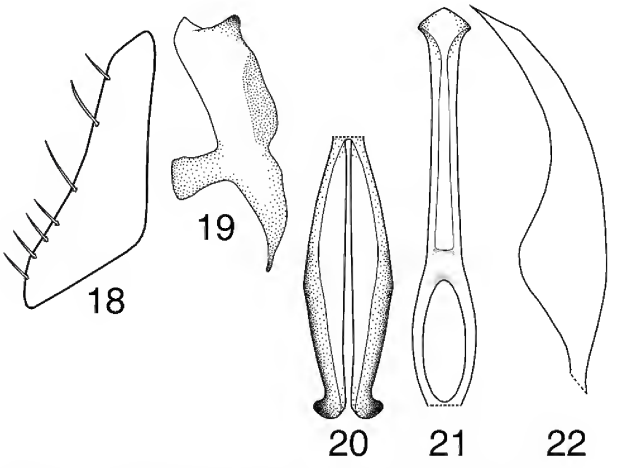
Distribution. Kosciuszko region, New South Wales.

Etymology. The specific name refers to the curvature of the aedeagal shaft being in the reverse direction from that in other known species of the genus.

Warlucephala abbreviata n.sp.

Figs. 3, 4, 7, 18–22

Type material. HOLOTYPE: ♂, Albany, Western Australia, x.1966, J.W. & F. Evans, AM K204211. PARATYPES: Western Australia: 12 specimens, same data as holotype: 1♀ mounted with holotype; 1♀ and 1, sex unknown (abdomen missing), mounted together; 1♂ (head missing) and 1♀, mounted together; 1♀ (mounted with tarsal remnants of second specimen which is not included in type series); 4♀♀ mounted individually (all in AM K204212–K204218, seven registration numbers for 10 specimens, some double-mounted); 1♂, 1♀ mounted individually (ASCU).



Figs. 18–22. Male genitalia of *Warlucephala abbreviata*: (*18*) subgenital plate; (*19*) paramere; (*20*) connective; (*21*) aedeagus, posteroventral view; (*22*) aedeagus, lateral view.

Description. *Size*. Brachypterous male (Fig. 3) (n=2) 3.2–3.4, brachypterous female (n=7) 4.0–4.3 mm, macropterous female (Fig. 4) (n=2) 4.2 mm. *Coloration*: Pale coffee brown. Face (Fig. 7) slightly darker toward margin with vertex, with faint pale lateral striping and short median pale band. Margin between face and vertex marked with cream band bordered on both sides with dark brown, this band convex laterally to reveal narrowly part of frontoclypeus when viewed dorsally. Vertex pale coffee with pale cream median stripe which continues less distinctly onto pronotum which also bears vague stripes laterally parallel to median. Tegmina pale translucent testaceous in brachypters, darker in cells of macropter. *Morphology*: Anteclypeus tapering base to apex, more strongly narrowed beyond lora which are widely separated from face margin. Vertex triangular, slightly convex, longer than wide between eyes, shagreen. pronotum short, obscurely transversely wrinkled. Tegmina short quadrate in brachypters, reaching to apex of abdomen in macropter which has appendix extending around apex of tegmen, apical cells long so that preapical cells are situated at around midlength of tegmen. First preapical cell short, rounded, third closed basally. *Male genitalia*: Pygofer of medium length, apically extended with rounded lobe bearing numerous macrosetae. Subgenital plates (Fig. 18) triangular, not nearly reaching as far posteriorly as pygofer with evenly spaced short macrosetae on concave outer margins. Parameres (Fig. 19) dark, short, broad, flattened, apically truncate to excavate. Connective (Fig. 20) with arms longer than main body. Aedeagus (Figs. 21, 22) with shaft evenly curved dorsally, tapered base to apex but slightly expanded apically with flange around gonopore.

Distribution. South Western Australia.

Etymology. The specific name refers to the strongly brachypterous tegmina found in most specimens.

Remarks. This species is more highly decorated than the other described species and is immediately recognisable by the markings on the vertex. The presence in the type series of a macropterous female indicates that polymorphism might also be a feature of other species of the genus.

Discussion

The placement of *Warlucephala* in Deltocephalini is based on the features used by Knight (1975) to define that tribe. These are the parallel arms of the aedeagal connective which is fused to the base of the aedeagus and the width of the genal strip below the lora. The new genus shows affinities with *Recilia* Edwards based on head structure, tegmen venation (as found in macropterous forms) and the simple, curved, tubular aedeagus with linear extension beyond the gonopore. It differs from *Recilia* in other features of the male genitalia, particularly the modified structure of the parameres, the occurrence of brachyptery, the flat vertex and the angulate margin between the vertex and the face.

Warlucephala has a Bassian distribution between the southwestern and southeastern portions of the Australian mainland. This contrasts with *Recilia* which is an Oriental genus distributed, within Australia, across the tropics with extensions into coastal temperate zones.

Brachyptery is common in Australian Deltocephalini with species of *Horouta* Knight and *Stenogiffardia parvula* (Kirkaldy) occurring commonly in brachypterous, semi-brachypterous or macropterous forms. Knight (1975) discussed the occurrence of brachyptery in *Horouta*, indicating that this form was normally restricted to the females and was typical of populations from higher altitudes. Fletcher (2004) demonstrated that brachyptery was common in both males and females. Males of *W. abbreviata* are only known in the brachypterous form and females in both forms while both males and females of *W. reversa* are semi-brachypterous. Although *W. reversa* is described above from the higher altitudes of the Kosciuszko region of NSW, *W. abbreviata* is only known at the low altitude of Albany, WA. Correlation between occurrence of brachyptery and higher altitudes therefore seems unlikely.

ACKNOWLEDGMENTS. Continuing work on the Australian Deltocephalinae was partially funded by a grant from the Australian Biological Resources Study, a component of the Australian Government Department of Environment and Heritage. Availability of the J.W. Evans leafhopper collection was made possible by the late Mrs Faith Evans and the Director of AM. Support for taxonomic research by NSW DPI is gratefully acknowledged.

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Munburra, A New Fly Genus from Tropical Australia (Empididae: Empidinae)

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ABSTRACT. *Munburra bulbicornis* n.gen and n.sp. (Diptera: Empididae: Empidinae) is described from the Cape York Peninsula, Queensland, Australia. This monotypic genus is distinguished by a large, raised ocellar triangle with enlarged ocelli, and two distinctive male secondary sexual characters, a greatly swollen postpedicel, and a long dorsoapical seta on a narrow unswollen leg I first tarsomere. Although it clearly belongs in the Hilarini, its relationship with other members of the tribe is unclear.

BICKEL, DANIEL J., 2006. *Munburra*, a new fly genus from tropical Australia (Empididae: Empidinae). *Records of the Australian Museum* 58(2): 129–132.

Australian species in the tribe Hilarini (Diptera: Empididae: Empidinae) are poorly known: there are many undescribed taxa in institutional holdings and probably many more awaiting field collection. This paper describes a new monotypic genus collected at numerous locales on Cape York Peninsula, primarily at light in tropical monsoonal woodlands. Males are distinctive in having swollen antennae and a strong dorsoapical seta on a narrow leg I basitarsus.

Materials and methods

This study is based on specimens borrowed from the Australian National Insect Collection, Canberra (ANIC), in large part from material collected during the Cape York Peninsula Land Use Survey (CYPLUS). Morphological terminology for the male terminalia is based on Cumming *et al.* (1995). Body length of males is measured from the base of the antennae to the tip of the abdomen. Wing length is the distance from the wing base to apex. The position of features on elongate structures such as leg segments is given as a fraction of the total length, starting from the base.

The relative lengths of the podomeres are representative ratios and not measurements. The ratios for each leg are given in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: *MSSC*, male secondary sexual character(s), the non-genitalic characters found only on male body; *I, II, III*, pro-, meso-, metathoracic legs; *C*, coxa; *T*, tibia; *F*, femur; *ad*, anterodorsal; *av*, anteroventral; *dv*, dorsoventral; *pd*, posterodorsal; *pv*, posteroventral; *t*, tarsus; t_{1-5}, tarsomeres 1 to 5.

Taxonomy

Genus *Munburra* n.gen.

Etymology. *Munburra* is a geographic place name near the Mt Webb, Queensland type locality. The name is of aboriginal origin, and the gender is here designated as feminine.

Type species. *Munburra bulbicornis* n.sp.

Diagnosis. Genus *Munburra*: subfamily Empidinae, tribe Hilarini, with the following characters: laterotergite usually bare; tibia I with anteroapical comb of 8–10 short even setae; cercus usually small and desclerotized, and fused laterally with the surstylus and epandrium; hypandrium usually forming a curved convex hood over the aedeagus along the distal margin; costa circumambient; vein R_1 swollen before it joins the costa.

Generic characters: ocellar triangle large and as rounded mound raised above surface of frons in both sexes; ocelli relatively large, well developed; male postpedicel slightly excavated at base, but basally inflated and tapering subtriangular; frons broad; thorax mostly orange yellow; male It_1 not swollen, but rather thin and slightly curved, with dorsal row of setae, and long curved dorsoapical seta, almost as long as tarsomere; Sc incomplete; R_{4+5} forked and R_4 with gentle S-shaped curve; hypopygium of the *Hilara-Hilarempis* type, with hypandrial keel narrow and covering aedeagus, cercus small and setose, and epandrium deeply split.

Remarks. *Munburra* is a monotypic genus from tropical monsoonal Australia with a single included species, *M. bulbicornis*. It is included in the tribe Hilarini (see Bickel, 1996) based on the characters listed in the Diagnosis, above. The genus is defined by the three apomorphies: a large, raised ocellar triangle with enlarged ocelli, and two distinctive male secondary sexual characters, a greatly swollen postpedicel, and a long dorsoapical seta on a narrow unswollen leg I first tarsomere. I have not seen these character states developed in other genera in the tribe.

Further, the Hilarini are more characteristic of temperate (both Northern and Southern Hemisphere) or montane habitats than the lowland tropics. Certainly many more taxa have been described from temperate regions, and although this may reflect regional collecting bias and/or the absence of netting along streams in the tropics, the Australian tropical fauna is indeed much poorer than that of southern Australia/ Tasmania. Therefore the presence of such an unusual genus in the tropics of Cape York Peninsula is of interest.

In some respects, *Munburra* appears similar to the genus *Sphicosa* Philippi, which comprises southern South American species and undescribed Australian species. Although *Sphicosa* is definitely in the tribe Empidini, the two genera appear to have a similar obliquely projecting proboscis (although in *Munburra* it can be elevated and depressed through the oral cavity, and is normally held in a vertical position), a costa reduced in thickness beyond R_{4+5}, and R_1 is not apically swollen. As well, the hypopygium of some male *Sphicosa* also have a keel-like hypandrium and appears almost hilarine-like. I regard these similarities as homoplasious, part of the suite of characters available for expression across the Empidinae, in both the Empidini and Hilarini.

Munburra bulbicornis n.sp.

Figs 1, 2

Type material. HOLOTYPE ♂, Queensland, Mt Webb NP, 3 km NE of Mt Webb, 15°03'S 145°09'E, 2.v.1981, at light, D.H. Colless. PARATYPES, 2♂♂, 4♀♀, same data as holotype, but variously from 30.iv to 2.v.1981 (ANIC).

Additional material. Queensland. ♀, 3 km W of Batavia Downs, 12°40'S 142°39'E, 17.i.1993, sweep, P. Zborowski; 2♂♂, 6♀♀, Batavia Downs, 12°39'S 142°42'E, 13–19.i.1993, at light, P. Zborowski, & 2♂♂, 2♀♀, 6–10.i.1993, 6–10.iii.1993, at light, I. Cunningham; 5♂♂, 8♀♀, Bertie Ck, 1 km SE of Heathlands, 11°49'S 142°30'E, 15–26.i.1992, at light, I.D. Naumann & T. Weir; 5♂♂, Cockatoo Ck, 17 km NW of Heathlands, 11°38'S 142°27'E, 15–26.i.1992, open forest, malaise trap, I.D. Naumann & T. Weir; ♂, 2♀♀, Davies Ck, 17 km SE of Mareeba, 17°01'S 145°35'E, 2.ii.1988, D. Rentz (all ANIC).

Description. *Male*. length: 2.3–2.4 mm; wing: 2.8× 1.1 mm. *Head* spheroidal, with dark brown cuticle; post-occiput, vertex, frons, face and gena covered with pale grey pruinosity; post-occiput convex; long postorbitals present on dorsal half of head; 2 pairs of vertical setae present, with outer pair stronger; only short postverticals present; ocellar triangle large and distinctly raised as rounded mound above surface of frons; ocelli relatively large, well developed; short setae present on ocellar triangle; pair of long diverging setae arising anteriad of lateral ocelli; frons broad, slightly wider than ocellar triangle, with 2–3 pairs of setae present mediad of lateral margin; eye facets of uniform size; eyes slightly notched laterad of antennae; face slightly wider than frons; female frons and face of similar width; face and clypeus relatively short; buccal cavity wide; palpus elongate, curved, slightly clubbed, with some long subapical dorsal and lateral setae; proboscis dark brown, length about head height, and projecting ventrally; antenna dark brown; scape and pedicel short; pedicel with some short apical setae; postpedicel slightly excavated at base, and basally inflated and tapering subtriangular; style aristate with short basal segment. *Thorax* almost entirely orange yellow, except for narrow brown stripe extending across mesonotum between ac band and extending onto scutellum, and lateral dark brown area just posteriad of mesonotal suture, and dorsad of wing base; setae dark brown; acrostichal setae (ac) short biseriate, with 10 pairs; dorsocentral setae (dc) present as three setae on posterior slope (two strong setae with shorter seta between), and extending anteriad as 11–12 short setae; 1 postalar seta, 2 postsutural supra-alar seta with some short setae anteriad, 3 short presutural intra-alar setae present; notopleuron with 2 strong posterior setae with 4–5 short hairs anteriad; 1 postpronotal seta present; pronotum with pair of diverging dorsal setae; proepisternum and laterotergite bare; scutellum with pair strong median setae, and pair of short laterals. *Legs* all coxae and remainder of legs pale yellow, with distal tarsomeres infuscated; major setae brown; coxae with long fine pale hairs; all tarsi with paired black claws and yellow pulvilli; CI with 2–3 distolateral setae I: 3.1; 3.2; 1.5/ 0.4/ 0.3/ 0.3/ 0.4; FI with row of longer pd setae; TI flattened anteroposteriorly, with mostly bare anterior and posterior surfaces, and with row of short dorsal setae (all MSSC); TI with anteroapical comb comprising 7–8 pale setae; It_1 not swollen, but rather thin and slightly curved, with dorsal row of setae, and long curved dorsoapical seta, almost as long as tarsomere (all MSSC); CII with some anterior and lateral setae; II: 3.1; 2.9; 1.2/ 0.4/ 0.3/ 0.3/ 0.4; FII with row long curved av setae; TII setose with some longer dorsal and ventral setae; CIII with 3 lateral setae and long posterior seta; III: 3.7; 3.5; 1.7/ 0.8/ 0.4/ 0.3/ 0.5; FIII also with row of longer av setae, and with row of long dorsal setae; TIII setose, with some longer dorsal and ventral setae, and with pair apical of av and pv spine-like setae; $IIIt_1$ with some long dorsal setae. *Wing* hyaline with brownish veins; costa circumambient, although reduced in thickness along posterior wing margin; costa with strong basal ad setae; Sc incomplete but approaching costa in some specimens; R_1 distally swollen before joining costa; R_{4+5} forked and R_4 with gentle S-shaped curve; stigma absent; crossvein closing anal cell (cell cup) strongly recurrent; distinct anal vein short but trace fold extending to margin; anal angle well developed; lower calypter yellow with short pale setae; halter yellow. *Abdomen* tergum1 narrow and mostly yellow; terga 2–7 brown; sterna mostly yellowish; vestiture yellow; terga 2–5 each with 2–3 lateral abdominal plaques;

hypopygium (Fig. 2b) mostly dark brown, but apical hypandrial keel yellow and almost translucent; cercus small and bearing 3 strong apical setae; hypandrium narrow, and covering aedeagus; aedeagus elongate and conforming to the curvature of the hypandrium; epandrium deeply split and setose, with external spine-like projection.

Female: similar to male except lacking MSSC, and as noted: frons width similar, and head (Fig. 2c) also with raised ocellar triangle; postpedicel not swollen; relative podomere ratio similar; TI not flattened, without row of dorsal setae, and without bare surface; tarsus I dark brown; It_1 straight, without dorsal row of setae, and lacking long dorsoapical seta; TIII not flattened; strong anal angle also present; abdominal terga gradually becoming narrow in width posteriad of segment 5.

Remarks. *Munburra bulbicornis* is known primarily from the monsoonal woodlands of Cape York Peninsula, Queensland. However, it has also been collected in mixed eucalypt forest/rainforest along Davies Creek, southeast of Mareeba, Atherton Tablelands. All specimens were collected between January and early May, during the rainy season and its immediate aftermath, when maximum surface water is present. *Munburra bulbicornis* is attracted to light, which might be correlated with the enlarged ocelli. Nothing is known of the species' mating behaviour, although other Hilarini are known to form horizontal swarms over water, often with male presentation of nuptial gifts (see Cumming, 1994).

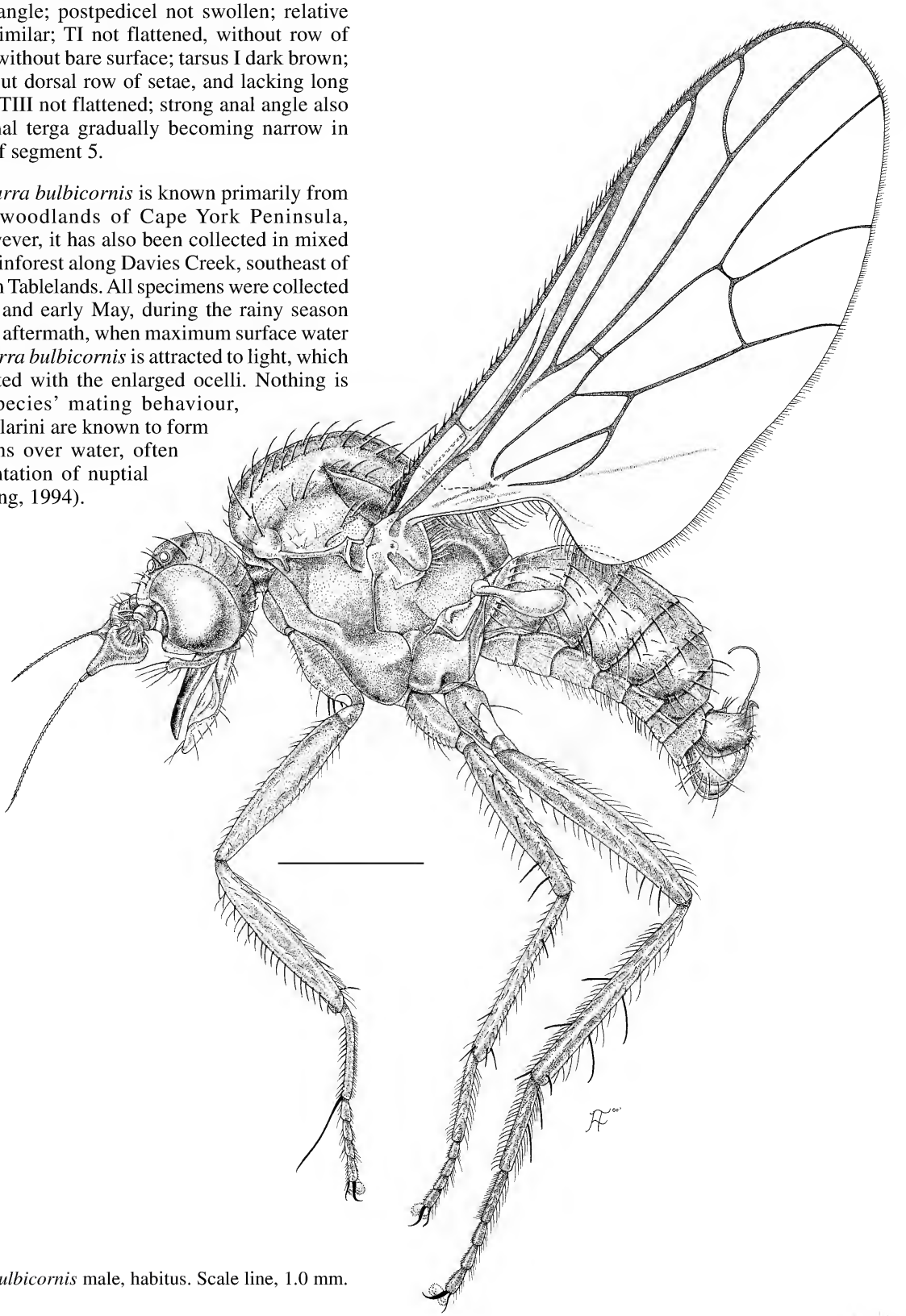

Fig. 1. *Munburra bulbicornis* male, habitus. Scale line, 1.0 mm.

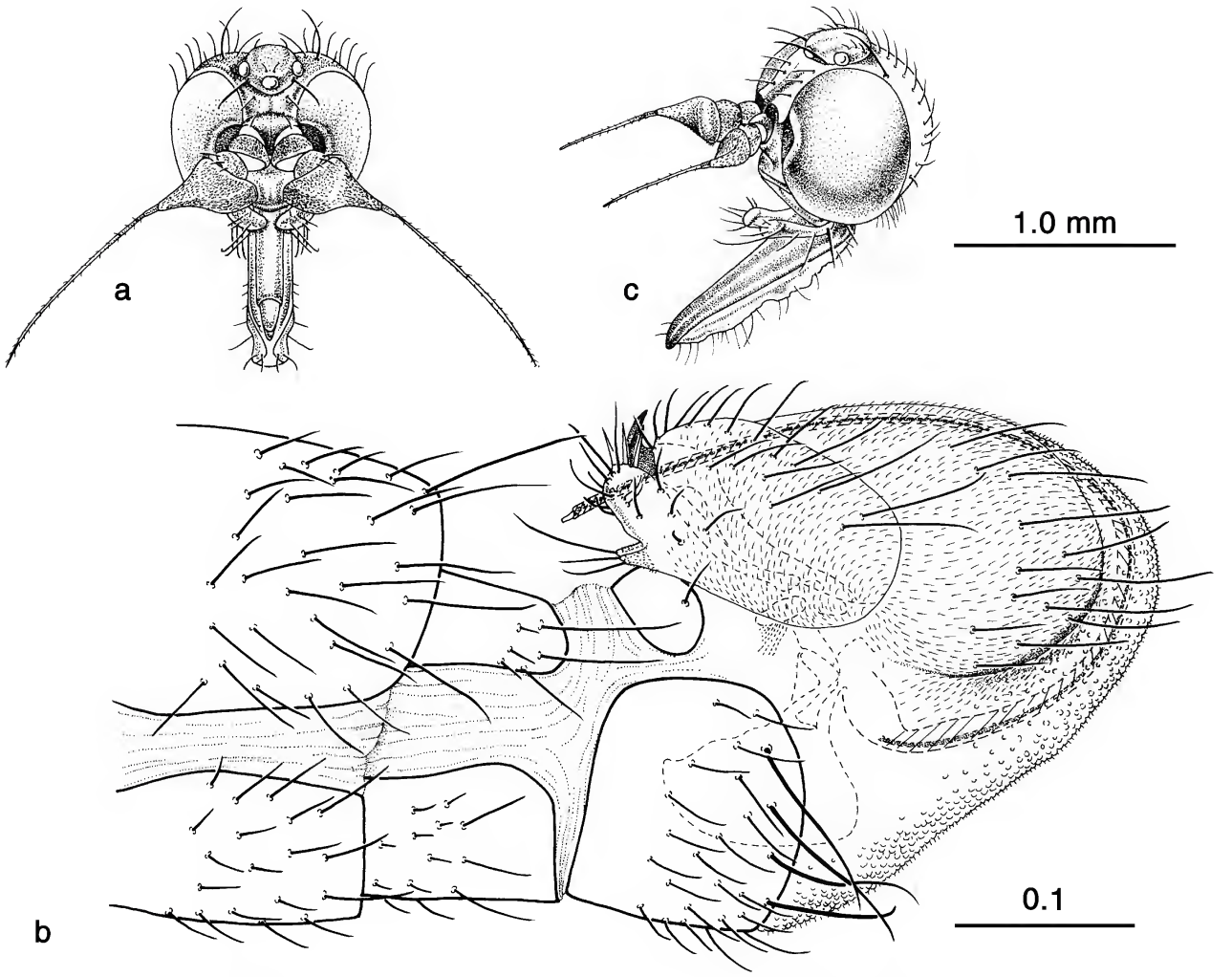

Fig. 2. *Munburra bulbicornis*, (*a*) male head, anterior; (*b*) male postabdomen, left lateral; (*c*) female head, anterolateral.

Notes on morphology and systematics

The following characters are useful in any phylogenetic analysis involving *Munburra*. Characters are given in the following format: "Character: plesiomorphic (ancestral) state/apomorphic (derived) state".

1 Ocellar triangle: unmodified/distinctly raised with enlarged ocelli. The ocellar triangle of *Munburra* is distinctly swollen and raised above the surface of the frons in both sexes, a condition that appears to be unique to the genus.

2 Postpedicel: unmodified/swollen in male. The postpedicel of *Munburra* is distinctly swollen in the male.

3 Male basitarsus I: unmodified/swollen or otherwise modified. Most male Hilarini (particularly the *Hilara-Hilarempis* complex of genera) have a swollen basitarsus I, which is known to have silk-producing glands in some taxa. However, in *Munburra*, the male basitarsus I is not swollen, but is thin and slightly curved and with a long dorsoapical seta, almost as long as the tarsomere. The *Munburra* male basitarsus I is unique to the genus, but its ancestral state could either be an unmodified tarsomere or the swollen *Hilara* type of basitarsus.

4 Vein Sc: complete/incomplete. This character is variable throughout the Empididae. The plesiomorphic condition is considered to be Sc complete and fusing with the costa.

ACKNOWLEDGMENTS. I thank P. Cranston (ANIC); for the loan of specimens. B. Sinclair provided useful comments on a earlier manuscript version. The figures were drawn by Hannah Finlay. This research was supported by Australian Research Council grant A19232651, for study of the systematics of Australian Empidinae.

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Taxonomic Revision of *Natatolana* (Crustacea: Isopoda: Cirolanidae)

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ABSTRACT. *Natatolana* Bruce, 1981 is one of the most speciose, widespread and abundant isopod genera occurring in marine environments. Species in the genus are ecologically important as scavengers and occasionally have a negative impact on commercial fisheries by feeding on catches restrained in traps, nets or on lines. The study of *Natatolana* species is hampered by difficulties in identification, inadequate descriptions and a lack of overall taxonomic revision. In this study, taxonomic, biogeographical and ecological information is reviewed for all 72 species of *Natatolana* now recognized worldwide. A revised generic diagnosis, a key to species, and diagnoses and synonymies for all species are presented. Phylogenetic relationships of the genus and species are discussed. Thirteen new species are described, 10 from Australia: *N. brucei* n.sp., *N. buzwilsoni* n.sp., *N. debrae* n.sp., *N. femina* n.sp., *N. flexura* n.sp., *N. helenae* n.sp., *N. lilliput* n.sp., *N. rusteni* n.sp., *N. sinuosa* n.sp., and *N. zebra* n.sp., and three from New Zealand: *N. aotearoa* n.sp., *N. honu* n.sp., and *N. paranarica* n.sp. Redescriptions or new illustrations are provided for an additional seven species. Lectotypes are designated for three species. Justification for placement of *N. lurur* and *N. wullunya* as junior synonyms of *N. arcicauda* and *N. nammuldi*, respectively, is presented.

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Introduction

Members of the family Cirolanidae are among the most abundant and speciose isopods of shallow marine environments as well as occurring in estuarine and freshwater habitats (Bruce, 1993a; Kensley, 1998; Bruce *et al.*, 2002). The family consists of approximately 61 genera, of these the most diverse are *Cirolana* and *Natatolana*, each with more than 70 nominal taxa, accounting for c. 36% of the known species in the family between them (Kensley *et al.*, 1996 onwards; this study).

Distribution, diversity and natural history. *Natatolana* is the most widespread genus in the family with species found across the range of latitudes and in all oceans other than the Arctic Ocean (Fig. 1). This genus is also more diverse in temperate and cold temperate waters than other cirolanid genera (Bruce, 1986) and apparently has its greatest diversity in the southwest Pacific (Bruce, 2003; Fig. 1). The high diversity in this region may reflect a bias in study (e.g., Bruce, 1986; Keable, 1997; Bruce & Olesen, 1995; Bruce, 2003; this study) relative to areas such as the coasts of Africa and South America but is valid when a comparison is made to areas where revisionary work has been undertaken, such as the North Atlantic and the tropical East Pacific (Brusca *et al.*, 1995; Keable & Bruce, 1997).

All species of *Natatolana* are restricted to marine, intertidal or subtidal environments; *N. natalis* has been collected from depths of c. 3,000 m while other species have been obtained from surface plankton (e.g., *N. amplocula*) or found stranded in pools on sand flats (e.g., *N. karkarook*). Specimens examined in this study, which could not be identified to species because of their poor condition, indicate that the genus occurs to depths of c. 6,000 m in the Peru–Chile trench (USNM 120961).The majority of species, however, are found at depths of less than 1,000 m.

Many species of *Natatolana* play an important role in ecosystems as scavengers (Keable, 1995, 1997; Ramsay *et al.*, 1997; Bozzano & Sarda, 2002; Castro *et al.*, 2005) with their response to carrion thought to be chemosensory, involving sensilla on the antennules and antennae (Wong & Moore, 1995; Kaïm-Malka *et al.*, 1998). This feeding strategy represents a potentially important mechanism for the dispersal of radioactive waste or other pollutants in the marine environment (Carvalho & Fowler, 1985). Species of the genus are also pests of commercial fisheries because they will feed on catches restrained in traps, nets or on lines (Hale, 1940; Bird, 1981; Bruce, 1986; Berrow, 1994; Mizzan, 1995). *Natatolana woodjonesi* has also been reported to attack and attempt to feed on SCUBA divers, causing superficial injuries (Edmonds, 1989).

Observations indicate the setose pereopods, which are an important taxonomic feature of the genus, are not used for swimming as previously suggested (Bruce, 1981) but provide protection for the pleopods during burrowing (Wägele & Bruce, 1989; see also Wetzer *et al.*, 1987; Keable, 1992; Taylor & Moore, 1995). Individuals are capable of

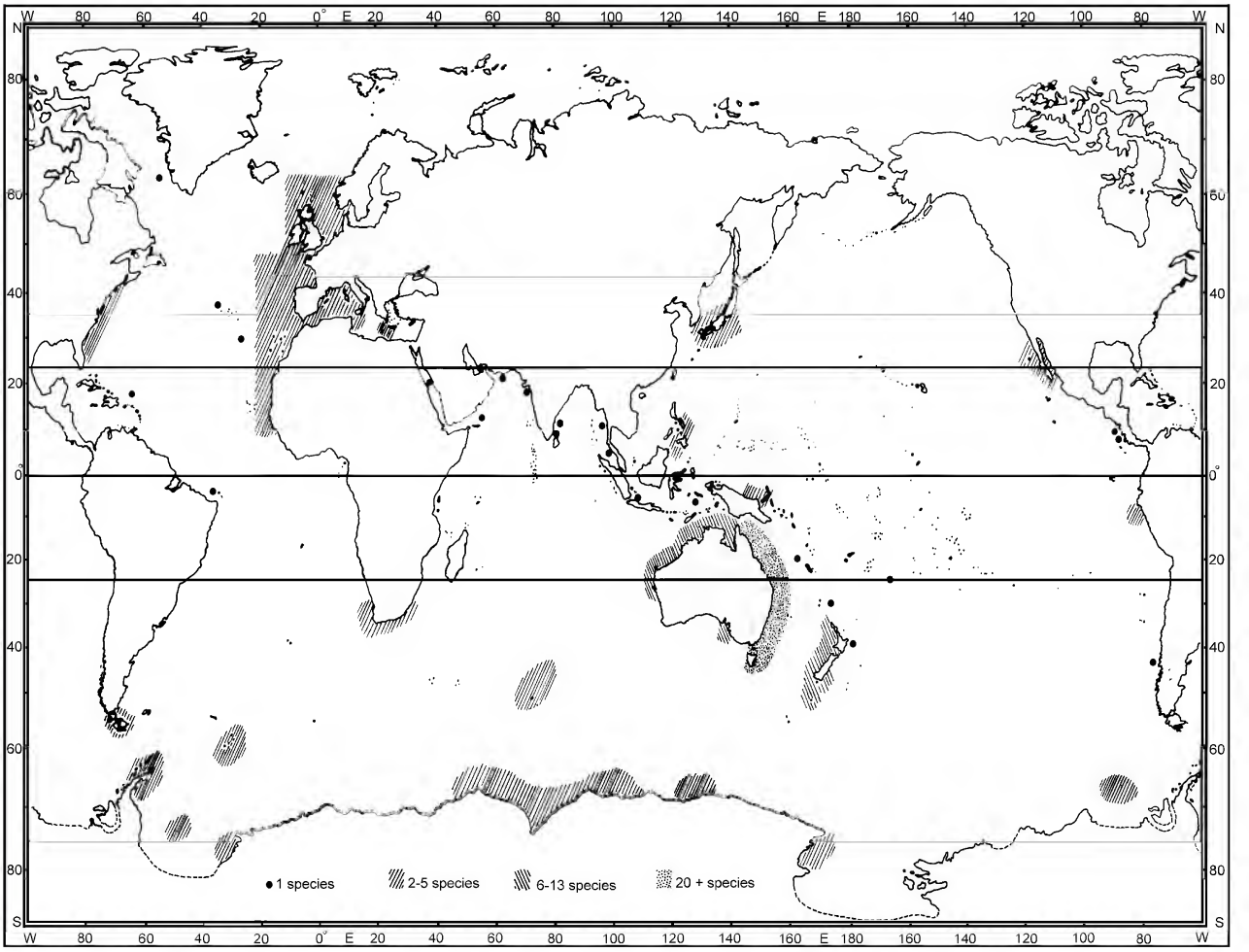

Fig. 1. World map indicating the distribution and diversity of described species of *Natatolana*.

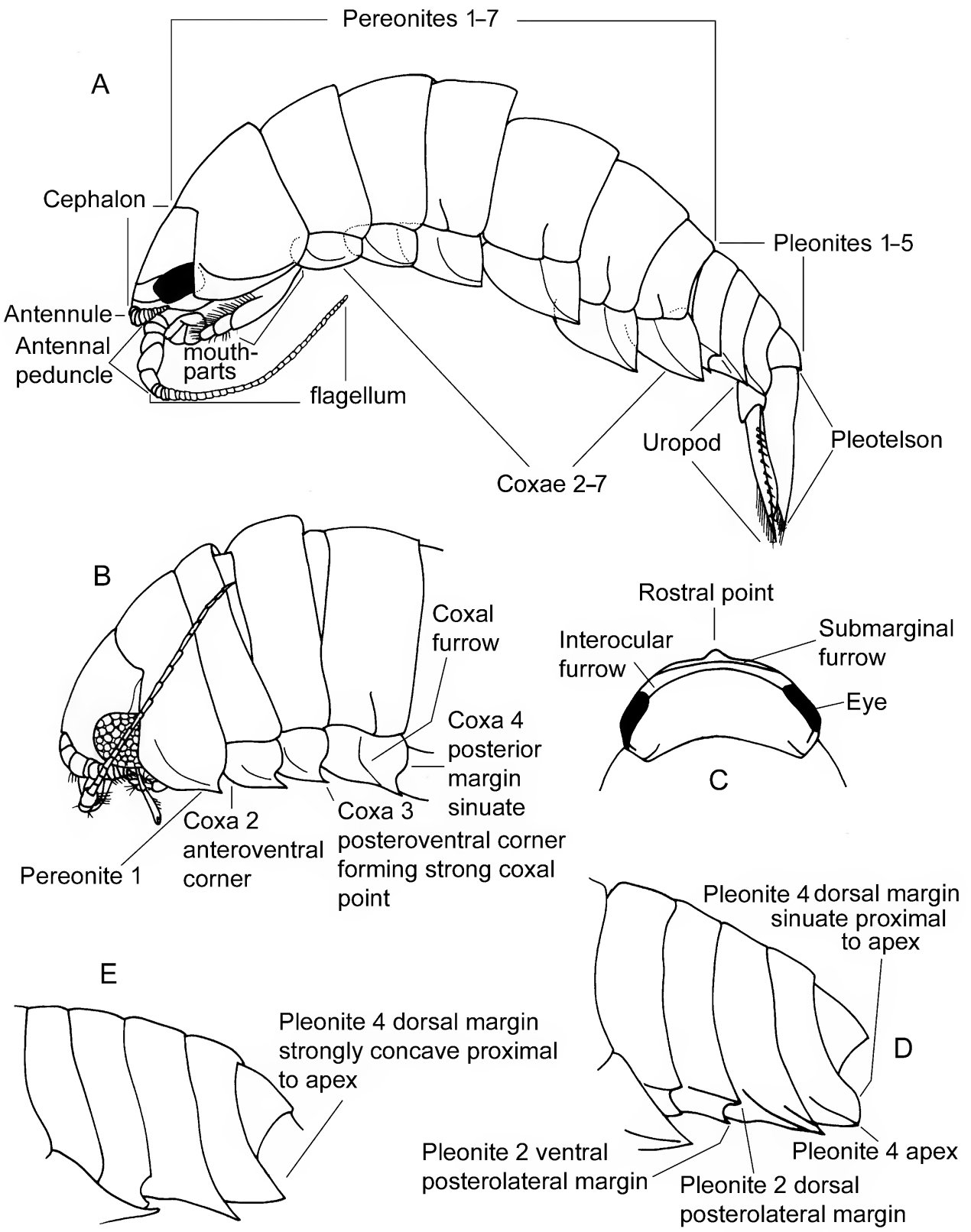

Fig. 2. Cirolanid characters referred to in text. (*A*) Lateral view of whole animal indicating basic body parts (pereopods occurring ventrally excluded). (*B*) Lateral view of anterior of body indicating terminology for coxae. (*C*) Dorsal view of cephalon. (*D*) Lateral view of pleonites indicating terminology. (*E*) Lateral view of pleonites showing pleonite 4 with a strongly concave dorsal margin proximal to apex.

swimming, however, by beating their pleopods (Wägele & Bruce, 1989; Keable, 1992; Macquart-Moulin & Kaïm-Malka, 1994; Taylor & Moore, 1995; Wong & Moore, 1995).

Scavenging species, such as *Natatolana tenuistylis*, are known to be restricted in distribution to sediments (Keable, 1992, 1995, this study) and Bruce (1986) considered that continental shelf sediments are the major habitat for species of *Natatolana*. At least one species (*N. albicaudata*), however, does not appear to feed as a scavenger and has been collected from coral rock and rubble rather than sediments (Bruce, 1995a).

Composition and taxonomic revision prior to this study. *Natatolana* was established by Bruce (1981) during redescription and rediagnosis of *Cirolana* Leach, 1818. Thirty-three species were assigned to *Natatolana*, all of which had previously been described and included in *Cirolana*. Prior to the study of Bruce (1981), Hansen (1890, 1905) had recognized resemblances among some of these species based on characters such as the elongate frontal lamina and large number of plumose setae on the posterior three pereopods (especially pereopod 7). The relationship of *Natatolana* to other genera was discussed by Bruce (1986), Botosaneanu *et al.* (1986), Wetzer *et al.* (1987), Wägele (1989) and Kensley & Schotte (1989) (see generic remarks).

The cirolanid isopod fauna of Australia was reviewed by Bruce (1986), providing redescriptions or new records of 10 previously described species and descriptions of 21 new species of *Natatolana*. Both Hansen (1905, p. 346) and Bruce (1986) noted the similarities among the species included in *Natatolana*, and the difficulty in making accurate identifications. Characters that are regarded as especially important for species recognition were discussed by Bruce (1986, p. 10). A revised list of the species of *Natatolana* was also included by Bruce (1986), with the addition of new species this totalled 56 species.

Subsequent publications providing redescriptions, new distribution records, new synonymies or describing new species of *Natatolana* include those of Brandt (1988), Kensley (1989), Kensley & Schotte (1989), Müller (1989), Wägele & Bruce (1989), Nunomura (1991), Hobbins & Jones (1993), Hutchings *et al.* (1993), Bruce (1995a), Bruce & Olesen (1995), Brusca *et al.* (1995), Keable (1995, 1996a, 1997), Mizzan (1995), Keable & Bruce (1997) and Bruce (2003). Saito *et al.* (2000) list the species *N. albicauda* (Nunomura, 1985) but this taxon (originally described in

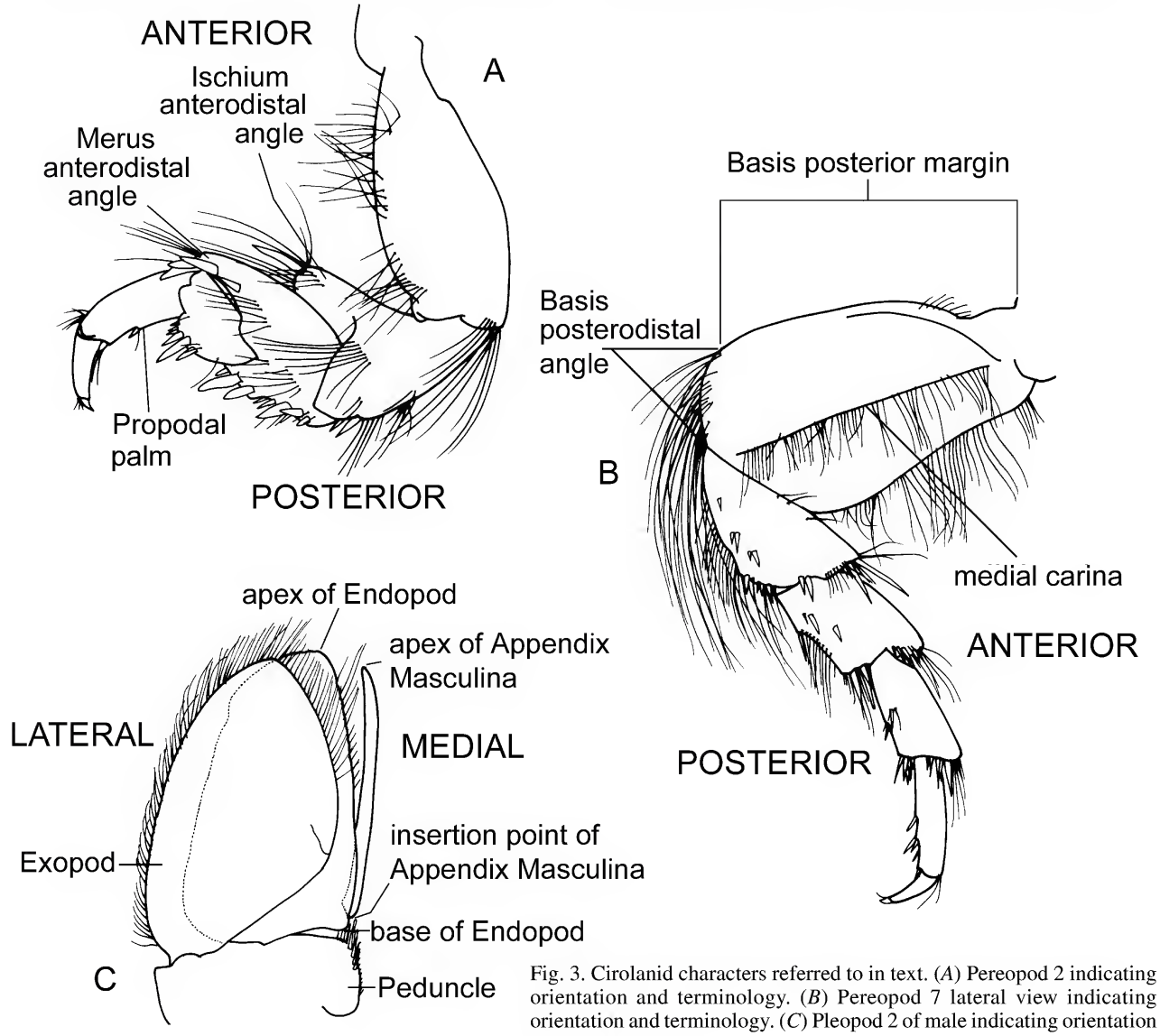

Fig. 3. Cirolanid characters referred to in text. (*A*) Pereopod 2 indicating orientation and terminology. (*B*) Pereopod 7 lateral view indicating orientation and terminology. (*C*) Pleopod 2 of male indicating orientation and terminology.

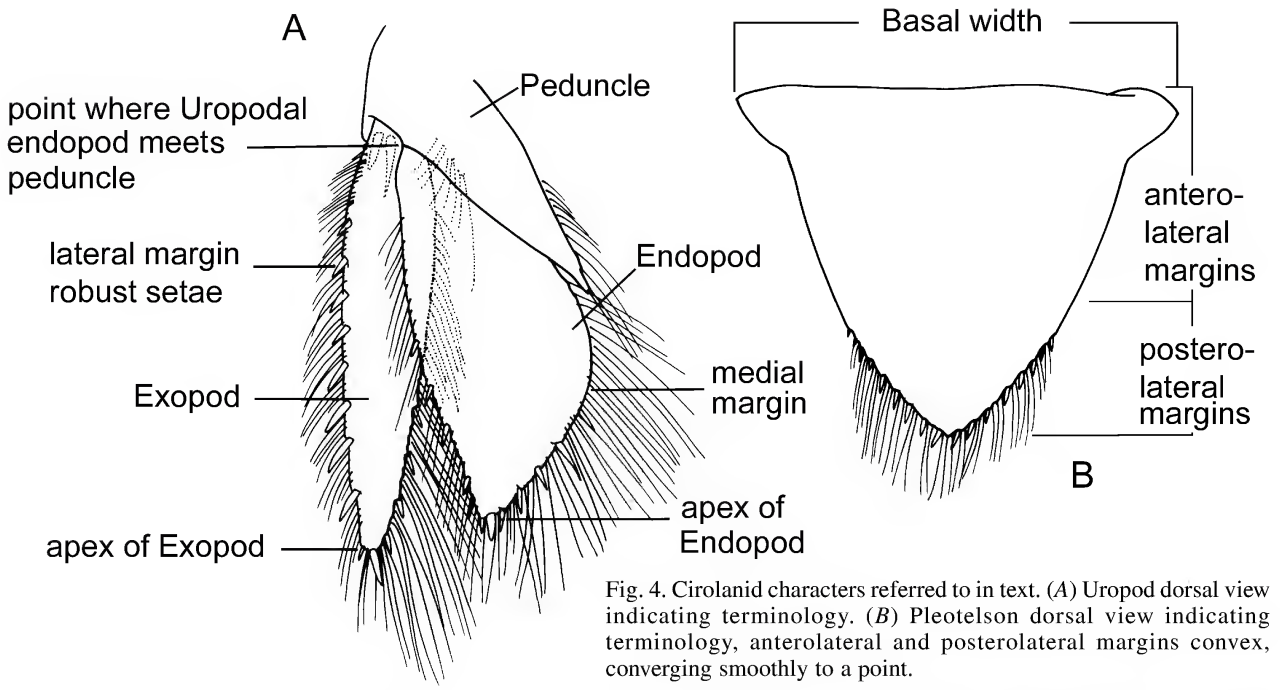

Fig. 4. Cirolanid characters referred to in text. (*A*) Uropod dorsal view indicating terminology. (*B*) Pleotelson dorsal view indicating terminology, anterolateral and posterolateral margins convex, converging smoothly to a point.

Cirolana) is a junior synonym of *Dolicholana elongata* (see Keable, 1999). Therefore, prior to this study, 62 described species of *Natatolana* were recognized.

Objective. Identification and study of species of *Natatolana* is hampered by the inadequacy of many of the existing descriptions and lack of a revisionary work which summarises existing knowledge for all species. This study addresses these problems by providing or reviewing taxonomic, biogeographical and ecological information for all 72 species of *Natatolana* now recognized. Redescriptions are presented for poorly known species where adequate material is available. New species from Australia and New Zealand which were recognized during the course of the study are described.

Materials and methods

Terminology and conventions. The anatomical terminology and the conventions regarding orientation of appendages follows that of Bruce (1986, 1993b) and outlined in Figs. 2–4, with modifications to terminology noted by Keable (1996a, 1997) and Keable & Bruce (1997). Practices for the examination and illustration of specimens are as outlined by Keable (1997). In the illustrations setules are indicated on the setae on which they were observed except for plumose setae on the proximal posterior pereopod segments and margins of the pleopod rami, pleotelson and uropods. The diagnoses and descriptions should be consulted for information of the distribution of these setae on these body parts. The relative extent of the antenna along the body noted in the species diagnoses was measured by flattening this appendage along the ventral margin of the body of the specimens examined. New species names are formed as nouns in apposition.

Electronic database. Morphological information recorded for the species diagnoses and descriptions, as well as information regarding the type material, sexual dimorphism, size range, character variation, distribution and ecology, has been recorded using the program DELTA (Dallwitz, 1980; Watson *et al.*, 1989; Dallwitz *et al.*, 1993). The edited copy provided here has been generated from this database. Data files from the database are available on request from the author.

Organization of species information

Type material and material examined. Type material examined is indicated under that heading. Other specimens examined for these species is noted under the heading "Material examined". Collection information additional to the type locality or absent in the original description of the species is indicated by use of square brackets under the heading "Type locality". In the descriptions of new species collection information that differs for the paratypes, from that of the holotype (i.e., as noted under type locality), is provided under the heading "Type material". In these descriptions the heading "Additional material" is used to indicate material excluded from the type series because it does not come from the type locality and/or was only identified after completion of the species descriptions.

Generally, the gender and number of specimens is not included for those collection lots for which there is abundant material. In other cases, the initial number before the registration number indicates the number of specimens in each lot. For material recorded from Australia, the state where the material is recorded from is given but not the country. A large amount of material used in this study has come from baited trap samples collected during the Scavengers of Eastern Australian Seas (SEAS) project directed by Dr J. Lowry (Crustacea Section, Australian Museum). To avoid repetition, collection data for this project is provided in summarized form only. The full data for this study is available via the Australian Museum specimen database.

Implicit characters

To avoid repetition of character states that apply to most but not all species of *Natatolana*, unless indicated otherwise, the following character states are implicit throughout the species diagnoses and descriptions presented here.

Diagnosis. *Eyes*: well developed; length less than 2× height. *Labrum*: smooth, without laminar projection. *Antenna*: flagellum digitate processes absent in males. *Coxal plates*: pereonite 1, coxa 2 posterior margins straight or slightly convex. Coxa 2 with anteroventral corner rounded. *Pleonite 2*: ventral posterolateral margin acute, formed into short process. *Pleonite 4*: posterodorsal margin sinuate, convex proximal to meeting ventrolateral margin at apex. *Pereopods 1–6*: males with the RS on the merus of pereopods 1–3, and carpus of pereopods 4–6, shorter than the propodus. *Pereopod 3*: ischium anterodistal angle produced subequal to that of pereopods 1–2. *Pereopods 5–7*: propodus long, but on pereopod 5 less than 2× the length of that of pereopod 7. *Uropods*: endopod lateral margin without prominent excision. Exopod lateral margin with RS.

Additional descriptive characters. *Cephalon*. Rostral point present, not prominent; submarginal cephalic furrow well developed, runs entire length of anterior margin. *Antennule*: short, not reaching pereonite 1; peduncle colinear; flagellum with aesthetascs present. *Antenna*: peduncular article 5 longer than article 4 and all other articles.

Mandible. Incisor broad. Molar process with RS present on margin. Palp article 2 with numerous SS. *Maxillule*: medial lobe lateral margin with a well-developed protuberance. *Maxilla*: lateral and middle lobe slender; medial lobe short and broad. *Maxilliped*: palp medial margin RS absent, SS along most of the length of articles 2–5, article 5 serrate setae present; lateral margin SS along most of the length of articles 2–5, PS absent.

Pleonites. 1–5 equally visible along dorsal margin. *Pleonites 1–2*: posterolateral margins produced, but not into distinct spiniform processes. *Pleonite 3*: posterolateral margins produced; acute.

Pleotelson smooth, ornamentation and sculpting absent; posterolateral margins not conspicuously serrate; PS restricted to posterolateral margins.

Pereopods 1–3 propodus posterodistal angle with 1 RS opposing dactylus. *Pereopod 7*: merus, carpus and propodus anterior margins without setae.

Pleopod 5 with proximal lobe of medial margin strongly produced.

Uropods. Peduncle medial margin strongly produced; exopod lanceolate.

Sexual dimorphism. Species of *Natatolana* exhibit little sexual dimorphism. All females differ from males in the primary sexual characters and do not have the pleopod 2 appendix masculina. Therefore, only differences other than these are recorded.

Distribution and ecology. Significant range extensions are underlined in the text. Ecological information is summarized where known but in most cases is limited to records of the species feeding as scavengers.

Abbreviations

Abbreviations of descriptive terms: *A1*, antennule; *A2*, antenna; *CE*, cephalon; *CL*, clypeal region; *FL*, frontal lamina; *MD*, mandible; *MP*, maxilliped; *MX1*, maxillule; *MX2*, maxilla; *n*, number of specimens; *P1–7*, pereopods 1–7; *PE*, penes; *PL1–5*, pleopods 1–5; *PN*, pleon; *PS*, plumose seta(e); *PT*, pleotelson; *RS*, robust seta(e); *SS*, slender seta(e); *U*, uropod.

AHF Allan Hancock Foundation, University of Southern California, USA;
AM The Australian Museum, Sydney;
BMNH The Natural History Museum, London, United Kingdom;
IOM Institut Océanographique Fondation Albert Ier Prince de Monaco;
LACM Natural History Museum of Los Angeles County, USA;
MNHN Muséum national d'Histoire Naturelle, Paris, France;
NIWA National Institute of Water & Atmospheric Research, New Zealand;
NMNZ Museum of New Zealand Te Papa Tongarewa, Wellington;
NMV Museum Victoria, Melbourne, Australia;
NTM Northern Territory Museum of Arts and Sciences, Darwin, Australia;
PMBC Phuket Marine Biological Center, Reference Collection, Thailand;
QM Queensland Museum, Brisbane, Australia;
SAM South African Museum, Cape Town;
SAMA South Australian Museum, Adelaide;
SIF Senckenberg Institute, Frankfurt, Germany;
SMNH Swedish Museum of Natural History, Stockholm;
TM Tasmanian Museum and Art Gallery, Hobart, Australia;
TSM Toyama Science Museum, Japan;
USNM National Museum of National History, Smithsonian Institution, Washington, D.C., USA;
WAM Western Australian Museum, Perth.
ZIAS Zoological Institute of the Academy of Science, St. Petersburg, Russia;
ZMB Zoological Museum, Berlin, Germany;
ZMG Zoological Museum of Göttingen, Germany;
ZMUA Zoological Museum, University of Amsterdam, Netherlands;
ZMUC Zoologisk Museum, University of Copenhagen, Denmark;

Taxonomy

Cirolanidae Dana, 1853

For a recent synonymy and emendations see Bruce (1986) and Brusca *et al.* (1995).

Natatolana Bruce, 1981

Natatolana Bruce, 1981: 957.–1986: 52.–Brusca & Iverson, 1985: 37.–Botosaneanu *et al.*, 1986: 412.–Wetzer *et al.*, 1987: 2.–Brandt, 1988: 102.–Kensley & Schotte, 1989: 139.–Brusca *et al.*, 1995: 74.–Yu & Li, 2001: 262.

Type species. *Cirolana hirtipes* Milne Edwards, 1840, by original designation [not subsequent designation as stated by Brusca *et al.* (1995)].

Diagnosis. *Cephalon*: width between 50–60% of pereonite 1; moderately to strongly enclosed laterally by pereonite 1; anterior margin smoothly rounded, or with rostral point, without smooth medial indentation; rostrum not prominent when present. *Frontal lamina*: forming an angle of c. 45° or less with clypeus; not fused to cephalon; elongate, length c. 3–10× basal width; ventral surface flat, not projecting anteroventrally from posterior. *Clypeus*: anterior margin abutting frontal lamina, ventral surface not projecting relative to frontal lamina. *Antennule*: colinear (most species), or geniculate (article 2 at right angles to article 1) (*N. vieta*). Peduncular articles 1–3 not fused; article 3 well developed,

longer than articles 1–2 or subequal to article 1. Accessory flagellum absent. Primary flagellum shorter than or subequal to peduncle; without callynophore. *Antenna*: not sexually dimorphic (most species), or sexually dimorphic; when dimorphic males with longer flagellae than females (*N. vieta*), or with digitate processes on flagellar articles (*N. insignis*). Peduncle of 5 articles; articles 1 and 2 shortest, subequal; article 4 subequal to article 3; article 5 longer than article 4 and all other articles, or subequal to article 4.

Mandible: molar well developed; medial surface smooth, without SS; RS present or absent on margins, numerous when present. Incisor broad, wider than narrowest part of mandible, or narrow, subequal to narrowest part of mandible; serrate; not quadridentate on left mandible. Lacinia mobilis absent. Setal row with numerous RS; intermediate SS absent. Palp 3-articulate; inserted slightly anterior to midlength, opposite molar; article 3 distally narrow. *Maxilla*: lateral lobe and middle lobe subequal; medial lobe short and broad; lateral lobe with 2–12 SS; middle and medial lobes with numerous setae. *Maxilliped*: palp medial margin with SS on more than half the length of articles 2–5; lateral margin with SS or PS along most of the length of articles 2–5; article 3 with distal margin width greater than proximal margin of article 4; article 4 with distal margin width greater than proximal margin of article 5. Endite with (most species) or without coupling hooks (*N. endota*, *N. karkarook*, *N. prolixa*, *N. buzwilsoni*).

Pereon: dorsal surfaces without setae; with (*N. amplocula*, *N. hirtipes*) or without indistinct tubercles (most species); with (*N. vieta*) or without wrinkle like furrows (most species); pereonite 1 longer than pereonite 2. *Coxae*: not forming sternal plates.

Pleonites: five unfused segments present; all equally visible along dorsal margin (most species), or pleonite 1 partially or completely concealed by pereonite 7 (*N. angula*, *N. boko*, *N. curta*, *N. hirtipes*, *N. imicola*, *N. intermedia, N. natalis*, *N. neglecta*, *N. obtusata*, *N. pilula*, *N. tenuistylis*, *N. valida*, *N. wowine*, *N. brucei*, *N. helenae*, *N. aotearoa*). *Pleonite 3*: epimera with lateral row of setae absent; posteroventral excision absent; enclosing or not enclosing pleonite 4. *Pleonite 5*: posterolateral margins encompassed by pleonite 4.

Pleotelson: dorsal surface with anterodorsal depression present or absent, otherwise smooth, setae, tubercles, pits and ridges absent; RS present or absent on margins; PS present or absent, when present moderately abundant, restricted to posterolateral margins, or sparse, restricted to apex; marginal teeth-like serrations absent.

Pereopods 1–7: dactylus with secondary unguis present or absent; secondary unguis not large or strongly sclerotized when present. *Pereopods 1–3*: ischium anterodistal angle produced subequally or noticeably reduced on pereopod 3. Merus anterodistal angle produced subequally. Dactylus shorter than propodus. *Pereopod 1*: merus anterodistal angle produced to posterodistal extent of carpus or beyond. *Pereopod 7*: basis noticeably broader in distal half compared to proximal half; anterior margin with long PS along entire length; medial carina with PS and SS along most of length of article; posterodistal angle with long PS present. Ischium anterior margin with PS and SS present or absent, PS sparse when present and only occurring distally; posterior margin with PS and SS present. Merus anterior margin SS present or absent, PS absent; posterior margin with PS and SS present or absent, PS sparse when present.

Penes: present or absent (vasa deferentia opening flush to surface of sternite 7); when present short and flattened, or long and tubular.

Pleopods: peduncle respiratory branchiae absent; accessory lobe reduced, without complex folding. Endopods 1–4 with PS on most of margins, 5 with only a few or no PS on margins; 1–4 without elongate laterally curving lobe arising from proximomedial angle. Exopods 1–4 without slender accessory lamella at posterior proximolateral angle. *Pleopod 1*: not operculate; peduncle length shorter than breadth; exopod and endopod broad, or only endopod narrow; exopod margin rounded, broad at apex; endopod width greater than 0.5× width of exopod. *Pleopod 2 appendix masculina*: arising basally or sub-basally; shorter or longer than endopod; broad, width equal to or greater than half pleopod peduncle length, or slender.

Uropods: inserted ventrolaterally on pleotelson; extending subequal to or beyond pleotelson, or not extending beyond pleotelson. Peduncle moderately or strongly produced along medial margin of endopod. Endopod and exopod margins with RS present or absent; PS on most of margin length; apices entire, not bifid or sub-bifid, with at least 2 RS. Endopod lateral margin with or without prominent lateral excision; without distinct pit.

Remarks. Kensley & Schotte (1989) placed *Natatolana* in the subfamily Conilerinae, based on the classification outlined by Botosaneanu *et al.* (1986). The subfamily divisions of the Cirolanidae, however, appear to be weakly defined and require revision through a phylogenetic analysis of the entire family, as suggested by Brusca *et al.* (1995) and Bruce (1995b). *Natatolana* is difficult to incorporate in phylogenetic analyses because of its diversity (Riseman & Brusca, 2002) and because no unique apomorphies have been proposed that define it (Wetzer *et al.*, 1987). The approach of using an exemplar for the genus presents difficulties because of polymorphism across the species. For example, Brandt & Poore (2003) use *N. woodjonesi* as a representative species in analysing suborder and superfamily relationships and characters. They score the pleopod 5 endopod as lacking setae whereas they are present in small numbers in several other species of *Natatolana* (Brandt, 1988, fig. 50; Brusca *et al.*, 1995; Keable, 1996b; this study, e.g., Fig. 28). It is an objective of this study to address some of these issues by clarifying character distribution within the genus and species identification.

Examination of specimens and descriptions of all species of *Natatolana* indicates that a putative synapomorphy that can unambiguously define the genus as a monophyletic group is the setation pattern on pereopod 7. This pattern entails the presence of long plumose setae on the length of the anterior margin and at the posterodistal angle of the basis, and the lack of plumose setae on the length of the anterior margin of the ischium. The plumose setae at the posterodistal angle of the basis are as long or longer than the ischium. This setation pattern is unique among the known taxa of the Cirolanidae (although it may occur in *Sintorolana*, a genus known only from a juvenile specimen in which pereopod 7 is missing). A similar setation pattern occurs in *Dolicholana elongata* but in this species plumose setae are present along the entire length of the anterior margin of the ischium and on the posterior margin of the merus. Of the species placed in *Natatolana*, plumose setae

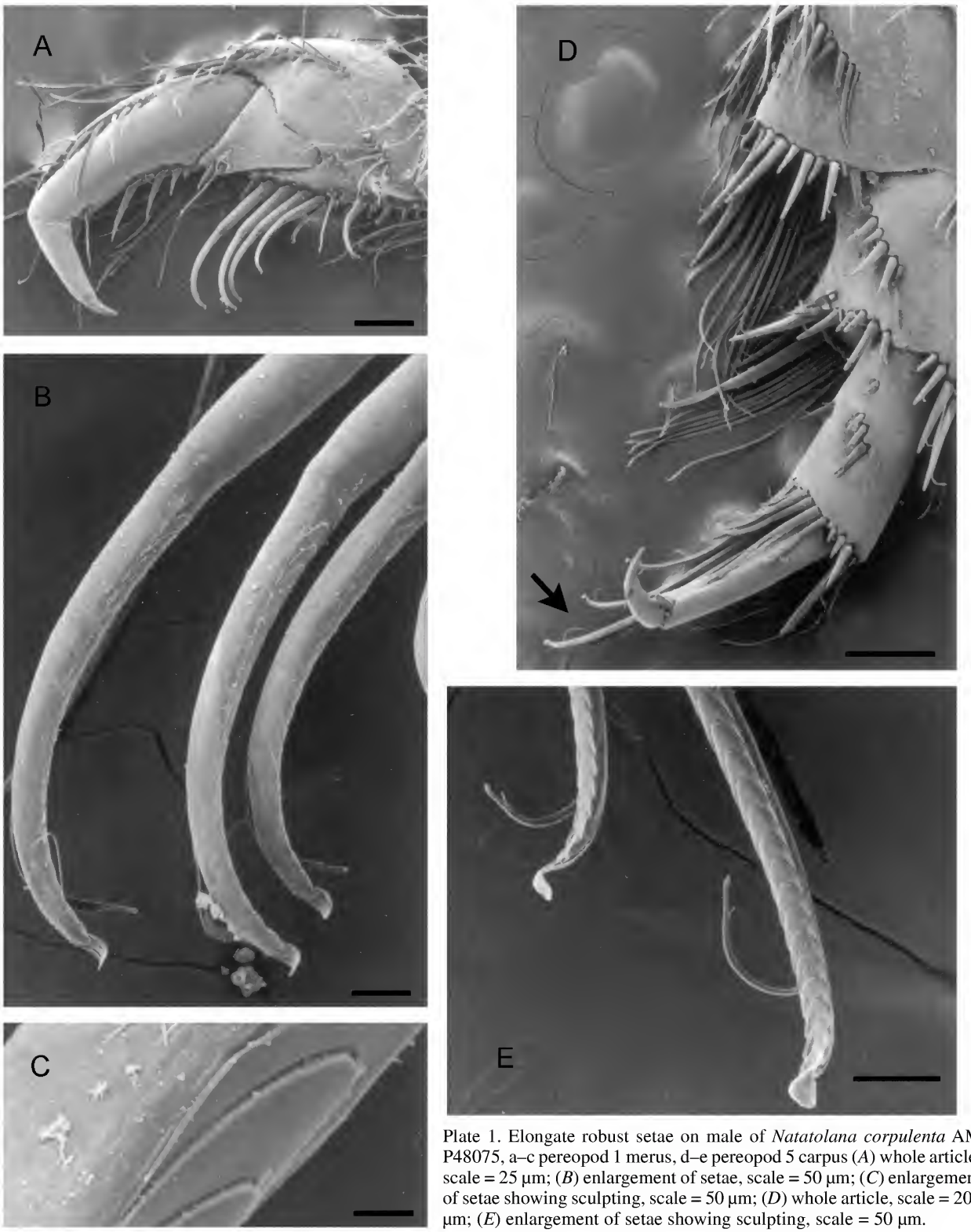

Plate 1. Elongate robust setae on male of *Natatolana corpulenta* AM P48075, a–c pereopod 1 merus, d–e pereopod 5 carpus (*A*) whole article, scale = 25 μm; (*B*) enlargement of setae, scale = 50 μm; (*C*) enlargement of setae showing sculpting, scale = 50 μm; (*D*) whole article, scale = 200 μm; (*E*) enlargement of setae showing sculpting, scale = 50 μm.

on the posterior margin of the ischium of pereopod 7 have only been observed in *N. angula, N. karkarook, N. narica* and *N. tenuistylis*. In these taxa these setae are sparse and do not extend all the way along this margin. In *D. elongata* plumose setae, however, are abundant and occur all the way along the margin. Only *N. boko* and *N. tenuistylis* are known to have plumose setae on the posterior margin of the merus of pereopod 7. Species of *Dolicholana* also differ from those of *Natatolana* in the characters noted below (Keable, 1999).

Other putative synapomorphies that may define *Natatolana* as a monophyletic group include: the smooth medial surface of the mandibular molar lacking slender setae (see Keable, 1996b; Keable, 1999); the short antennule in which the flagellum is shorter than, or subequal in length to the peduncle with articles broader than longer; and the narrow frontal lamina lacking a posteroventral projection.

Comparison of these additional synapomorphies to characters occurring in other genera suggest, however, that they are not unique and further analysis is necessary before their phylogenetic significance can be fully evaluated.

The composition, relationships and phylogenetic significance of the four existing informal groups (the *N. albicaudata*, *N. pellucida*, *N. valida* and *N. woodjonesi* groups—Bruce, 1986; Wägele & Bruce, 1989) within *Natatolana* are unclear because characters used in defining them may not be shared by all members of the group and/or may be shared by species excluded from the group. For example, ambiguous characters used in defining these groups include:

- entire or complete coxal furrows—these occur in species placed in both the *N. albicaudata* and *N. pellucida* groups;
- pereopod 2 lacking robust setae on the palm of the propodus—this is a condition that occurs in all species included in both the *N. pellucida* and *N. woodjonesi* groups;
- pereopod 7 basis narrow with margins straight—this state occurs in the *N. pellucida* group and is indistinguishable from the state described for the *N. valida* group (pereopod 7 basis narrow, broadening distally, margins nearly straight).

Furthermore, conflicting statements have been made regarding the composition of the informal groups within *Natatolana* and some of the characters used in formulating them. For example, *N. rossi* and *N. hirtipes* have been included in the *N. valida* group, which is characterized by having "coxal plates with furrows feeble or absent", despite *N. rossi* and *N. hirtipes* being differentiated from *N. matong* on the grounds that they have "distinct" or "conspicuous" coxal furrows (Bruce, 1986, p. 97). Also, many species do not readily fall into these groups (Bruce, 1986; Bruce & Olesen, 1995; this study).

A robust phylogenetic analysis of *Natatolana* is, therefore, required to determine the utility of these groups. A relevant character that has not been highlighted previously is the development of long, modified, robust setae on the posterior margins of the merus of pereopods 1–3 and on the distal margin of the carpus of pereopods 4–6 (Plate 1). These specialized setae are only known to occur on males of the species Bruce (1986) placed in the *N. pellucida* group (*N. pellucida, N. corpulenta, N. galathea, N. laewilla, N. longispina*) and *N. debrae* n.sp., *N. sinuosa* n.sp. and *N. zebra* n.sp. This and other characters included in the species diagnoses presented here, however, were used in a phylogenetic analysis by Keable (1996) that was inconclusive (being both ambiguous and partially resolved) regarding species relationships within *Natatolana*. The main conclusions of this analysis were that morphological characters are difficult to use because of problems in defining enough character state transitions to resolve relationships. This was viewed as being possibly the result of a strong adaptation to the benthic/scavenging niche, resulting in a conservative morphology, and/or particular speciation processes. Consequently, study of functional morphology of species of *Natatolana* to further resolve morphological character states and use of molecular techniques to clarify patterns of speciation within the genus were suggested to aid progress in determining species relationships.

Material examined during this study indicates the need to place *Natatolana lurur* Bruce, 1986 and *N. wullunya* Bruce, 1986 in synonymy with *N. arcicauda* Holdich, Harrison & Bruce, 1981, and *N. nammuldi* Bruce, 1986, respectively. Therefore, 59 previously described species are recognized and, with the addition of 13 species described here, the total number of species now in the genus is 72.

Key to species of *Natatolana*

Although some species can be identified using only female specimens, the key is written under the assumption that a fully adult male specimen is being used. Male specimens are preferable for identification because they have additional diagnostic characters (e.g., penes, appendix masculina) not found in females.

Due to uncertainty regarding many character states in *N. anophthalma* and *N. pallidocula*, they are not included in the key. Couplets to which they may key (based on their descriptions) are indicated using symbols † and ‡ respectively. Comparisons of these species to those identified in the marked couplets are given at the end of the key.

Diagnostic characters are highlighted in bold text in some of the longer couplets which utilize additional characters to aid in identification.

1 Uropod endopod, lateral margin with prominent deep excision (e.g., Fig. 30) 2

—— Uropod endopod, lateral margin without prominent excision 3

2 Coxae, all with furrows present; pleotelson with 4–6 robust setae on posterolateral margins; penes absent in males, vas deferens opening flush with the surface of sternite 7 ..... *N. variguberna*

—— Coxae 2–5 without furrows; pleotelson with 10–14 robust setae on posterolateral margins; penes present in males ..... *N. honu* n.sp.

3 (*a*) Pleotelson with distinct dorsal depression (e.g., Fig. 47) 4

—— (*b*) Pleotelson without distinct dorsal depression; pereopod 7, basis with the distance between the medial carina and the anterior margin less than between medial carina and the posterior margin 15

—— (*c*) Pleotelson without distinct dorsal depression; pereopod 7, basis with the distance between the medial carina and the anterior margin greater than between medial carina and the posterior margin 48

4 Antennule, peduncular articles 1–2 geniculate; antennal flagellum extending at least to pleon ..... *N. vieta*

—— Antennule, peduncular articles 1–2 colinear; antennal flagellum not extending to pleon 5

5 Pereopod 3, propodal palm with robust setae; penes absent in males, vas deferens opening flush with the surface of sternite 7 ..... ‡ † *N. natalensis*

—— Pereopod 3, propodal palm without robust setae; penes present in males ..... * 6

6 Pleotelson, apex strongly produced, posterolateral margins straight or concave and noticeably less convex than anterolateral margins (e.g., Fig. 47) 7

—— Pleotelson, apex not strongly produced, posterolateral margins convex and joining smoothly with anterolateral margins (e.g., Fig. 53) 10

7 Coxa 2, anteroventral corner produced into an acute tooth (Fig. 13) ..... ‡ *N. corpulenta*

—— Coxa 2, anteroventral corner rounded 8

8 Pereonite 1 and coxa 2 with sinuate posterior margins, posteroventral corners developed into acute coxal points (e.g., Fig. 45) 9

—— Pereonite 1 and coxa 2 with straight or slightly convex posterior margins, posteroventral corners rounded ..... ‡ *N. femina* n.sp.

9 Pereonite 1 and coxa 2 with the posteroventral corners developed into strong coxal points (Fig. 45) ..... *N. sinuosa* n.sp.

—— Pereonite 1 and coxa 2 with the posteroventral corners developed into weak coxal points (Fig. 14) ..... *N. debrae* n.sp.

10 Pleotelson, posterolateral margins with 2 robust setae; uropod endopod, lateral margin slightly concave with a prominent notch (Fig. 22) ..... † *N. flexura* n.sp.

—— Pleotelson, posterolateral margins with 8 or more robust setae; uropod endopod, lateral margin convex without a prominent notch 11

11 **Eyes vestigial, ommatidia indistinct and weakly pigmented**; coxae, all with furrows or some without furrows; coxa 2, posteroventral corner strongly rounded so that posterior margin appears shorter than anterior margin ..... † *N. laewilla*

—— **Eyes well developed, ommatidia distinct and strongly pigmented**; coxae, all with furrows; coxa 2, posteroventral corner not strongly rounded 12

12 Pereonite 1 and coxa 2 with sinuate posterior margins, posteroventral corners developed into acute coxal points (e.g., Fig. 45) ..... *N. longispina*

—— Pereonite 1 and coxa 2 with straight or convex posterior margins, posteroventral corners slightly rounded (e.g., Fig. 51) 13

13 Pereopod 5, propodus elongate (twice length of pereopod 7 propodus) (Figs. 52–53) ..... *N. zebra* n.sp.

—— Pereopod 5, propodus short (less than twice length of pereopod 7 propodus) (e.g., Figs. 26–27) 14

14 Pleotelson width at posterior third greater than half basal width, posteroventral margins strongly convex; uropod endopod relatively broad, width greater than half length of lateral margin ..... *N. galathea*

—— Pleotelson width at posterior third less than half basal width, posteroventral margins weakly convex; uropod endopod relatively narrow, width less than half length of lateral margin ..... *N. pellucida*

15 Antennal flagellum longer than body 16

—— Antennal flagellum shorter than body 17

16 Pleotelson, margins straight, robust setae present ..... *N. endota*

—— Pleotelson, margins sinuate, robust setae absent ..... *N. prolixa*

17 Pleotelson, margins without robust setae ..... † 18

—— Pleotelson, margins with robust setae 19

18 Pleotelson, posterolateral margins concave and meeting at a narrowly rounded apex; appendix masculina, apex bluntly rounded ..... *N. boko*

—— Pleotelson, posterolateral margins convex and meeting at a truncate apex; appendix masculina, apex with digitate process ..... *N. pilula*

19 **Males with penes**; interocular furrow incomplete or absent; coxal furrows present on all coxae; pereopods 2 and 3, propodal palms with robust setae 20

—— **Males without penes**; interocular furrow complete, incomplete or absent; coxal furrows present on all, some or none of the coxae; pereopods 2 and 3, propodal palms with or without robust setae 30

20 Pleonite 4, posterodorsal margin strongly concave proximal to meeting ventrolateral margin at apex (e.g., Fig. 5) ..... ‡ 21

—— Pleonite 4, posterodorsal margin sinuate, convex proximal to meeting ventrolateral margin at apex (e.g., Fig. 25) 25

21 Eyes rounded, length less than twice height; appendix masculina in males straight or only very slightly curved laterally (e.g., Fig. 27) 22

—— Eyes elongate, length approximately twice height; appendix masculina in males strongly curved or twisted laterally 24

22 Pleonite 2, dorsal posterolateral margin strongly projecting posterior to ventral posterolateral margin; appendix masculina, apex bluntly rounded 23

—— Pleonite 2, dorsal posterolateral margin projecting subequal to ventral posterolateral margin; appendix masculina, apex tapered to finely acute point ..... *N. pastorei*

23 Eyes with light pink pigment (fading with preservation), approximately 9 vertical and 10 horizontal ommatidia; pleotelson, apex not strongly produced, posterolateral margins convex and joining smoothly with anterolateral margins; pereopod 7, basis posterior margin with sparse setae proximally and distally or with setae completely absent ..... *N. meridionalis*

—— Eyes with dark red or black pigment (generally not fading with preservation), c. 17 vertical and 12 horizontal ommatidia; pleotelson, apex strongly produced, posterolateral margins concave and distinctly angled to anterolateral margins; pereopod 7, basis posterior margin with relatively dense setae present on entire length ..... *N. oculata*

24 Coxa 2, anteroventral corner produced into an acute tooth (e.g., Fig. 13); pleotelson, anterolateral margins straight, angled to posterolateral margins ..... *N. nitida*

—— Coxa 2, anteroventral corner rounded; pleotelson, anterolateral margins convex and joining smoothly with posterolateral margins ..... *N. intermedia*

25 Eyes well developed, ommatidia distinct, with dark pigment (generally not fading with preservation); pleotelson posterolateral margins straight, distinctly angled to anterolateral margins 26

—— Eyes vestigial, ommatidia indistinct, lacking pigment (possibly fading with preservation); pleotelson posterolateral margins convex, joining smoothly with anterolateral margins 27

26 Adults of small size, c. 8 mm in length; appendix masculina slender and strongly curved laterally ..... ** *N. gracilis*

—— Adults of large size, to over 25 mm in length; appendix masculina broad and distinctly twisted ..... *N. obtusata*

27 Appendix masculina slender, margins smooth, apex bluntly rounded 28

—— Appendix masculina broad, margins with a distinct notch or projection near apex 29

28 Appendix masculina strongly curved laterally ..... † *N. californiensis*

—— Appendix masculina slightly curved laterally ..... *N. bowmani*

29 (*a*) Appendix masculina, apex rounded and proximal margin of distal notch blunt; pleotelson usually with 12 or less robust setae; pereopods 1–2 propodal palm with fewer than 5, 3 robust setae respectively; uropod exopod lateral margin with fewer than 8 robust setae ..... *N. imicola*

—— (*b*) Appendix masculina, apex rounded and proximal margin of distal notch blunt; pleotelson usually with 12 or more robust setae; pereopods 1–2 propodal palm with 5, 3 or more robust setae respectively; uropod exopod lateral margin with 8 or more robust setae ..... *N. rekohu*

—— (*c*) Appendix masculina, apex acute and proximal margin of distal notch with an acute projection ..... *N. natalis*

30 Eyes elongate, length approximately twice height; pereopods 2 and 3, propodal palms with robust setae; pleotelson, posterolateral margins with at least 10 robust setae 31

—— Eyes short, length approximately equal to height, or vestigial; pereopods 2 and 3, propodal palms with or without robust setae; pleotelson, posterolateral margins with more than or less than 10 robust setae 37

31 Appendix masculina broad, margins strongly curved laterally, apex truncate (Fig. 50) ..... ‡ *N. virilis*

—— Appendix masculina slender, margins straight or slightly curved laterally, apex bluntly rounded (e.g., Fig. 28) ..... ‡ 32

32 Appendix masculina distinctly shorter than endopod ..... *N. nukumbutho*

—— Appendix masculina subequal to, or longer than, endopod length 33

33 Frontal lamina, apex strongly expanded (broader than posterior margin) 34

—— Frontal lamina, apex weakly expanded (width equal to, or narrower than, posterior margin) ..... *N. valida*

34 Pleonite 4, posterodorsal margins strongly sinuate, distinctly convex proximal to meeting ventrolateral margin at apex 35

—— Pleonite 4, posterodorsal margins weakly sinuate, indistinctly convex proximal to meeting ventrolateral margin at apex ..... *N. matong*

35 Coxal furrows present on all coxae 36

—— Coxal furrows present on anterior coxae only ..... *N. carlenae*

36 Eyes, anterior margin angled, sloping posteriorly from dorsal margin to ventral margin; interocular furrow smoothly convex (Fig. 25) ..... *N. hirtipes*

—— Eyes, anterior margin convex; interocular furrow produced anteromedially (Fig. 41) ..... *N. rossi*

37 **Pleonite 4, posterodorsal margin strongly concave proximal to meeting ventrolateral margin at apex** (e.g., Fig. 5); interocular furrow complete (e.g., Fig. 5) 38

—— **Pleonite 4, posterodorsal margin sinuate, convex proximal to meeting ventrolateral margin at apex** (e.g., Fig. 25); interocular furrow complete or incomplete 41

38 Uropod exopod longer than endopod 39

—— Uropod exopod distinctly shorter than endopod 40

39 Pleotelson, posterolateral margins broadly rounded, approximately parallel to basal margin at apex; uropod endopod, medial margin sinuate ..... *N. narica*

—— Pleotelson, posterolateral margins convex, not parallel to basal margin at apex; uropod endopod, medial margin smoothly convex ..... *N. paranarica* n.sp.

40 Frontal lamina, lateral margins straight and parallel; pereopod 3, ischium anterodistal angle extending subequal to that of pereopods 1 and 2 (e.g., Fig. 26) ..... *N. thurar*

—— Frontal lamina, lateral margins straight and narrowing anteriorly; pereopod 3, ischium anterodistal angle distinctly less extended than that of pereopod 1 and 2 (Fig. 6) ..... *N. aotearoa* n.sp.

41 (*a*) Eyes well developed, ommatidia distinct; interocular furrow developed into a distinct ridge; uropod exopod length subequal to endopod ..... *N. japonensis*

—— (*b*) Eyes vestigial, ommatidia indistinct; interocular furrow developed into a distinct ridge; uropod exopod length distinctly shorter than endopod 42

—— (*c*) Eyes well developed with distinct ommatidia; interocular furrow not developed into a distinct ridge; uropod exopod length distinctly shorter than endopod 43

42 *Interocular furrow* complete; pleotelson, anterolateral margins convex and joining smoothly with posterolateral margins; pereopod 3, ischium distinctly less extended than that of pereopods 1 and 2 (e.g., Fig. 6) ..... † *N. caeca*

—— *Interocular furrow* incomplete, anteriorly deflected; pleotelson, anterolateral margins straight and distinctly angled to anterolateral margins; pereopod 3, ischium extended subequal to that of pereopods 1 and 2 (e.g., Fig. 26) ..... † *N. gorung*

43 Maxilliped, palp lateral margin with plumose setae on articles 2–5; pleotelson, apex truncate (forming a line parallel with basal margin) ..... *N. helenae* n.sp.

—— Maxilliped, palp lateral margin with slender setae on articles 2–5; pleotelson, apex forming an angle or rounded 44

44 **Uropod endopod broadly rounded distally, medial margin extending posterior to endopod apex**; pleotelson, posterolateral margins broadly rounded (convex and smoothly continuous with anterolateral margins approximately parallel to basal margin at apex); pereopods 2 and 3, propodal palms with robust setae 45

—— **Uropod endopod lanceolate, medial margin not extending posterior to endopod apex**; pleotelson, posterolateral margins broadly rounded or not broadly rounded; pereopods 2 and 3, propodal palms with or without robust setae 48

45 Antennal flagellum of males with digitate processes at anterolateral margin of articles; uropod endopod, lateral margin with distinct notch ..... *N. insignis*

—— Antennal flagellum of males without digitate processes; uropod endopod, lateral margin without distinct notch 46

46 Maxilliped, endite without coupling hooks; maxillule, endopod with simple robust setae lacking setules ..... *N. buzwilsoni* n.sp.

—— Maxilliped, endite with coupling hooks; maxillule, endopod with pappose robust setae 47

47 *Interocular furrow* complete ..... *N. amplocula*

—— *Interocular furrow* incomplete ..... *N. curta*

48 Labrum with acute laminar projection ..... *N. karkarook*

—— Labrum smooth 49

49 Antenna at least 0.5× as long as the body; pleonite 2, ventral posterolateral margin strongly projecting posteriorly to dorsal posterolateral margin; pleonite 4, posterodorsal margin strongly sinuate meeting ventral margin at a small point ..... *N. tenuistylis*

—— Antenna less than 0.5× as long as the body; pleonite 2, ventral posterolateral margin projecting subequally, or anteriorly, to dorsal posterolateral margin; pleonite 4, posterodorsal margin sinuate but not meeting ventral margin at a small point 50

50 **Appendix masculina, apex with acute projection**; interocular furrow incomplete; coxal furrows distinct on all coxae, never discontinuous; pleotelson, posterolateral margins with fewer than 8 robust setae; pereopod 7, basis posterior margin with setae present; uropod exopod, lateral margin with robust setae present 51

—— **Appendix masculina, apex with projection forming a Y shape or bluntly rounded**; interocular furrow complete, incomplete or absent; coxal furrows distinct on all or only some coxae, sometimes discontinuous; pleotelson with fewer or more than 8 robust setae; pereopod 7, basis posterior margin with setae present or absent; uropod exopod, lateral margin with robust setae present or absent 52

51 Coxal furrows extending completely across coxae 4–7; pleotelson, posterolateral margins convex and joining smoothly with anterolateral margins; pereopod 7, basis posterior margin with dense setae along entire length ..... *N. gallica*

—— Coxal furrows extending only about 50 to 75% of the way across coxae 4–7; pleotelson, posterolateral margins straight or only slightly convex and noticeably angled to anterolateral margins; pereopod 7, basis posterior margin with sparse setae ..... *N. thalme*

52 Pereopods 2 and 3, propodal palms with robust setae 53

—— Pereopods 2 and 3, propodal palms without robust setae 57

53 **Appendix masculina, lateral margin projecting, apex formed into a Y shaped process**; interocular furrow incomplete; coxal furrows distinct on anterior coxae only; pereopod 7, basis posterior margin with setae present on entire length ..... *N. borealis*

—— **Appendix masculina, margins smooth, apex bluntly rounded not forming a Y shaped process**; interocular furrow complete, incomplete or absent; coxal furrows distinct on anterior coxae only, or on anterior and posterior coxae; pereopod 7, basis posterior margin with setae restricted to proximal half or absent 54

54 **Appendix masculina strongly curved laterally, forming semi-circle**; interocular furrow absent; pleotelson, posterolateral margins straight and distinctly angled to anterolateral margins ..... *N. gracilis* **

—— **Appendix masculina straight or only slightly curved laterally**; interocular furrow complete or incomplete; pleotelson, posterolateral margins straight and distinctly angled to anterolateral margins, or convex and joining smoothly with anterolateral margins 55

55 Coxal furrows distinct, continuous on all coxae; basis of pereopod 7 broad, width greater than 0.5× length, posterior margin without setae 56

—— Coxal furrows indistinct, discontinuous or absent on coxae 4, 5 and 6; basis of pereopod 7 narrow, width less than 0.5× length, posterior margin with setae on proximal quarter ..... *N. arcicauda*

56 *Interocular furrow* complete ..... *N. albicaudata*

—— *Interocular furrow* incomplete ..... *N. chilensis*

57 Pleotelson, posterolateral margins straight and meeting at angular apex 58

—— Pleotelson, posterolateral margins convex or concave 60

58 Pleotelson, posterolateral margins distinctly angled to anterolateral margins; antennal peduncular article 4 without a row of long slender setae along entire posterolateral margin 59

—— Pleotelson, posterolateral margins joining smoothly with anterolateral margins; antennal peduncular article 4 with a row of long slender setae along entire posterolateral margin ..... *N. lowryi*

59 Pleotelson, posterolateral margins meeting at an acute angle; pereopod 7, basis with anterior margin distinctly sinuate (distance between anterior margin and medial carina greater than between posterior margin and medial carina) and posterior margin with setae along entire length ..... *N. luticola*

—— Pleotelson, posterolateral margins meeting at an obtuse angle; pereopod 7, basis with anterior margin slightly convex (distance between anterior margin and medial carina less than between posterior margin and medial carina) and posterior margin without setae ..... *N. neglecta*

60 Pleotelson, posterolateral margins concave ..... *N. brucei* n.sp.

—— Pleotelson, posterolateral margins convex 61

61 *Interocular furrow* complete and pleotelson with at least 8 robust setae on margins ..... *N. angula*

—— *Interocular furrow* complete and pleotelson with less than 8 robust setae on margins, or interocular furrow incomplete and pleotelson with a maximum of 8 robust setae on margins 62

62 **Frontal lamina, lateral margins straight and narrowing anteriorly**; pleotelson posterolateral margins with 4 robust setae; uropod exopod lateral margin with robust setae absent ..... *N. arrama*

—— **Frontal lamina, lateral margins medially constricted**; pleotelson posterolateral margins with 4 or more robust setae; uropod exopod lateral margin with robust setae present or absent 63

63 Uropod exopod less than 80% length of endopod 64

—— Uropod exopod greater than 85% length of endopod 67

64 Uropod exopod, lateral margin with robust setae present 65

—— Uropod exopod, lateral margin with robust setae absent ..... *N. bulba*

65 Antennal flagellum with more than 19 articles extending to the posterior of pereonite 3 ..... *N. taiti*

—— Antennal flagellum with less than 19 articles, not extending beyond pereonite 2 66

66 (*a*) **Interocular furrow complete**; **pleotelson length less than basal width**, posterolateral margins usually with 4 robust setae ..... *N. lilliput* n.sp.

—— (*b*) **Interocular furrow incomplete**; **pleotelson length less than basal width**, posterolateral margins usually with 4 robust setae ..... *N. kahiba*

—— (*c*) **Interocular furrow incomplete**; **pleotelson length greater than basal width**, posterolateral margins usually with 6 robust setae ..... *N. rusteni* n.sp.

67 Appendix masculina, apex falcate; antenna reaching to posterior of pereonite 3; pleonite 4, posterodorsal margin broadly rounded, apex not angled; uropod endopod, apex rounded ..... *N. wowine*

—— Appendix masculina, apex bluntly rounded; antenna reaching to posterior of pereonite 2; pleonite 4, posterodorsal margin rounded, apex angled; uropod endopod, apex acute 68

68 Pleotelson, apex distinctly produced, margins usually with 4 (occasionally with 6) robust setae; uropod endopod, lateral margin angled at midpoint with each half approximately straight ..... *N. woodjonesi*

—— Pleotelson, apex indistinctly produced, margins usually with 8 (occasionally with 6) robust setae; uropod endopod, lateral margin slightly sinuate in larger specimens ..... *N. nammuldi*

* Although no adult males of *Natatolana femina* are known, based on the presence of other characters in female specimens, fully adult males are predicted to have penes.

** Because of uncertainty regarding the presence or absence of penes in *N. gracilis*, it is included twice in the key.

Couplet 5 *Natatolana pallidocula* has more angled posterolateral margins of the pleotelson than *N. natalensis*. In *N. anophthalma* the eyes are vestigial or absent, whereas they are well developed in *N. natalensis*.

Couplet 7 *Natatolana pallidocula* has rectangular eyes with 14 ommatidia in the horizontal row, whereas *N. corpulenta* has oval eyes with c. 5 ommatidia in the horizontal row (see remarks for *N. corpulenta*).

Couplet 8 *Natatolana pallidocula* has rectangular eyes with 14 ommatidia in the horizontal row, whereas *N. femina* has oval eyes with c. 5 ommatidia in the horizontal row.

Couplet 10 *Natatolana anophthalma* apparently lacks robust setae on the pleotelson posterolateral margins (although they may have rubbed off), and the prominent notch on the uropod endopod lateral margin, which are present in *N. flexura*.

Couplet 11 *Natatolana anophthalma* apparently lacks robust setae on the pleotelson posterolateral margins (although they may have rubbed off), whereas they are present in *N. laewilla*. Examination of the holotype of *N. anophthalma* is needed to determine further differences to *N. laewilla* but these may include complete coxal furrows on all coxae in *N. anophthalma*.

Couplet 17 *Natatolana anophthalma* apparently lacks robust setae on the pleotelson posterolateral margins (although they may have rubbed off) but can be separated from *N. boko* and *N. pilula* by the smoothly convex posterolateral margins of the pleotelson meeting at a point.

Couplet 20 *Natatolana pallidocula* can be separated from all species identified from couplet 20 by its elongate eye, concave posterodorsal margin of pleonite 4, angular posterior pleotelson margins and straight appendix masculina.

Couplet 28 Examination of the holotype of *N. anophthalma* is needed to distinguish it from *N. californiensis* although *N. anophthalma* is described as lacking robust setae on the pleotelson.

Couplet 31 *Natatolana pallidocula* apparently has the pleotelson with a more acute apex than in any of the species identified from couplet 31.

Couplet 42 *Natatolana pallidocula* apparently has well-developed coxal furrows on all coxae, while these are absent on at least some coxae in both *N. caeca* and *N. gorung*.

Species of *Natatolana*

Natatolana albicaudata (Stebbing, 1900)

Cirolana albicaudata Stebbing, 1900: 631, pl. lxviiB.–Nierstrasz, 1931: 152.

Cirolana albicaudata var. *japonica* Thielemann, 1910: 8, figs. 1–4.–Nierstrasz, 1931: 152.

Cirolana albicauda japonica.–Iwasa, 1965: 14, 18.

Natatolana albicaudata.–Bruce, 1981: 958.–1986: 71, figs. 46, 47.–1995a: 409 figs. 19F,G.–Brusca *et al*., 1995: 79.–Kensley, 2001: 230.–Bruce *et al*., 2002: 148.

Natatolana albicaudata japonica.–Saito *et al*., 2000: 64.

Not *Cirolana albicaudata*.–Barnard, 1936: 152, fig. 2a–c [mis-identification = *Natatolana insignis* Hobbins & Jones, 1993].

Not *Cirolana albicaudata*.–Richardson, 1910: 5 [mis-identification = *Natatolana amplocula* Bruce, 1986].

Type material. Syntypes: 4♂♂, 3.8–5.3 mm, 2♀♀, 3.9, 4.2 mm, 5 mancas, 2.0–3.8 mm, BMNH 1906.4.19:44-54 (examined). • Type locality: Barawon, Blanche Bay, New Britain [Papua New Guinea, c. 6°S 150°E].

Material examined. **Queensland**: series from Lizard Island, Qld., 14°40'S 145°28'E, N. Preston: manca, QM W18917, 30 Dec. 1986; ♀, QM W18912, 9 Nov. 1987, stn 2; manca, QM W18913, 4 Dec. 1987, stn 2; manca, QM W18910, 30 Oct. 1987, stn 1. **New Caledonia**: ♀, ZMUC CRU137, 23°32'S 167°36'E, surface, Dana Station 3604, 24 Nov. 1928.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.4× as long as body, reaching to between the posterior of pereonite 2 and 4 (In the original description it is illustrated as extending to posterior of pereonite 4 and described as about half the length of the body. This agrees with the syntype specimens examined here. The redescription of Bruce [1986] states that it extends to the anterior of pereonite 3 but is variable and may extend to pereonite 5). *Coxal plates*: furrows strongly developed, on coxae 2–7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.84× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 7–10 RS (the original description and figures indicate 8, Bruce's (1986) redescription gives 9 or 10 and his figures show 7). *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopods 5–7*: propodus long, on pereopod 5 greatly elongate, 2× that of pereopod 7. *Pereopod 7*: basis broad, width 0.6× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.94× length of endopod; slender; margins very slightly curved laterally; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.78× the length of the endopod.

Size. The largest syntype specimen is 5.3 mm, Bruce (1986) recorded specimens to 8.9 mm.

Remarks. Bruce (1986, p.53, 74) noted that *Natatolana albicaudata*, *N. amplocula* and *N. curta* share a number of similarities but that *N. albicaudata* can be distinguished from all other species in the genus by a combination of characters. These include having chromatophores, conspicuously elongated dactyls, a slender propodus on pereopods 4–6, and other characters dealing with the frontal lamina, pereopods, pleotelson and uropods, coxal furrowing and pleon shape that were not elaborated on. Both *N. curta* and *N. amplocula* were originally known only from single specimens. Comparison of the types and additional specimens of all three species indicates that the characters used by Bruce (1986) to differentiate them are difficult to apply. Type specimens of *N. albicaudata*, however, differ from those of *N. amplocula* and *N. curta* most noticeably in having a less rounded uropod endopod and pleotelson. It also appears to be a smaller species in which indistinct tubercles do not form on the dorsal surface of the pereonites of males and has fewer robust setae on the uropod exopod. Further collections of *N. albicaudata*, *N. amplocula* and *N. curta* from their type localities would help confirm this, especially as the type material of *N. albicaudata* is in poor condition, and Bruce (1986) indicated that in material he identified, which is larger than the type material, the apices of the pleotelson and uropods are far more distinctly rounded.

Richardson (1910) identified material from the Philippines as both *Natatolana albicaudata* and *N. curta* but did not indicate differences between these species. Examination of the material Richardson identified as *N. albicaudata* indicates it is most similar to *N. amplocula*.

The specimens reported here from Lizard Island and New Caledonia are only tentatively identified because of the difficulties in differentiating this species (noted above) and because the material consists of a limited series of females and juveniles.

Distribution and ecology. Records are restricted here to Japan (Thielemann, 1910; Iwasa, 1965), northwestern and northeastern Australia (Bruce, 1986), Indonesia (Nierstrasz, 1931), Papua New Guinea (Stebbing, 1900; Bruce, 1995a), and New Caledonia. This range is tentative given the similarities with *N. amplocula* and *N. curta*. Hayward *et al*. (1999, 2001) report *N. albicaudata* from New Zealand but Bruce (2003) considered this a probable misidentification. From surface plankton to a depth of 250 m (Thielemann, 1910).

Natatolana albicaudata is not a scavenger. Bruce (1995a) has briefly discussed the ecology of this species, noting that it has not been collected in Madang Lagoon using baited traps but does occur there. It has also been collected from coral rock and rubble rather than particulate substrata.

Natatolana amplocula Bruce, 1986

Natatolana amplocula Bruce, 1986: 74, fig. 48.–Brusca *et al*., 1995: 79.–Bruce *et al*., 2002: 149.

Cirolana albicaudata.–Richardson, 1910: 5 [mis-identification, not *N. albicaudata* Stebbing, 1900].

Type material. Holotype: female, 13.2 mm, ZMUC CRU1691 (examined). • Type locality: south of Kei Islands, 5°34'S 132°26'E.

Material examined. **Philippines**: 3♂♂, USNM 40959, Tomindao Island anchorage, electric light, Albatross Expedition, 26 Feb. 1908 [reported by Richardson (1910)]; 5♂♂, 7♀♀, USNM 40988, Java Island anchorage, electric light, Albatross Expedition, 14 Dec. 1908 [reported by Richardson (1910)]; 3♀♀, ZMUC CRU118, Tubajon Bay, Dinagat, 10°20'N 125°32'E, corals, 40 m, 16 Jul. 1951, Galathea Station 414. **Indonesia**: ♂, ZMUC CRU128, Banda Sea, 6°37'N 122°24'E, planktonic, 3 April 1929, Dana stn 3684; 57, ZMUC CRU127, off Java, 6°41.5'S 105°19.5'E, planktonic-surface, 3 Sep. 1929, Dana stn 3808. **Australia, Northern Territory**: ♂, NTM Cr005812, New Year

Island, 10°55'S 133°01'E, 5m. **Queensland**: ♂, ♀, manca, AM P47471, Shadwell Reef, 11°27.66'S 143°46.63'E, nightlight, surface over 20 m depth, H. Larson, J. Leis, M. McGrouther, 12 Jan. 1993, QLD-646; series from west of Carter Reef, 14°33'S 145°35'E, surface over 30 m (neuston and vertical tows), J. Leis & party, RV Sunbird, 4–7 Mar. 1983: 2♂♂, 4♀♀, AM P47472; 2♀♀, 3 mancas, AM P47473; ♂, 5♀♀, AM P47474; ♀, AM P47475; ♀, QM W18911, Lizard Island, 14°40'S 145°28'E, N. Preston, 12 Nov. 1986, stn 1; ♂, AM P47476, off East Fitzroy Reef, 23°34.92'S 152°11.76'E, 58 m, 16–17 Jun. 1993, SEAS QLD-952. **Western Australia**: 5♂♂, ♀, NMV J37011, North-West Shelf between Port Hedland and Dampier, 18°45'S 118°24'E, trawl, 142 m, G.C.B. Poore & H.M. Lew-Ton, 5 Jun. 1983. **Southwest Pacific Ocean**: 2♀♀, AM P47477, Elizabeth Reef, Tasman Sea, 29°55'S 159°05'E, hand net at surface, attracted to light at night, A. Gill & J.K. Lowry on RV Flamingo Bay, 12 Dec. 1987, site 42; ♂, ♀, AM P41150, Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone and sand bottom, 244 m, 1.2 m sled, J.K. Lowry *et al.* on RV Franklin, 2 May 1989, FRO589-8; ♂, damaged specimen, MNHN, New Caledonia, 19°07'S 163°22'E, 200 m, MUSORSTOM 4, 14 Sep. 1985, stn 0151; ♂, MNHN, Chesterfield Islands, 22°47.7'S 159°23.7'E, 360–390 m, MUSORSTOM 5, 11 Oct. 1986, stn 0299; ♀, 2 mancas, NMNZ, Raoul Island, Kermadec Islands, 28°50'S 177°48'E, plankton net at surface over 268–332 m, RV James Cook, 17 Jun. 1976.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing posteriorly. *Antenna*: c. 0.4× as long as body, reaching to between the posterior of pereonite 3 and posterior of pereonite 4. *Coxal plates*: furrows strongly developed, on coxae 2–7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.74× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins broadly rounded; apex produced into a small point; with 6–12 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis broad, width 0.6× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.85–0.95× length of endopod; slender; margins bent slightly medially; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.73× the length of the endopod; lateral margin convex.

Variation. The number of robust setae on the pleotelson is most often 8 but may range between 6 and 12 (6 in the holotype and specimens from Lizard Island, Queensland; eight in specimens from the Philippines [USNM 40988], Carter Reef and Shadwell Reef, Queensland; 10 in specimens from the Philippines [USNM 40959], Taupo Seamount and New Caledonia; 12 in specimens from northwestern Australia and the southwest Pacific [Elizabeth Reef, Raoul Island and Chesterfield Islands]. Indistinct tubercles are present on the dorsal surface of pereonites 1 and 3 in males from off Java, Indonesia, New Year Island, NT, Carter Reef and east Fitzroy Reef, Queensland, New Caledonia and Taupo Seamount. The antennae reach the posterior of pereonite 4 in the material from Carter Reef and Elizabeth Reef whereas in other material they extend approximately half way along pereonite 3.

Sexual dimorphism. Males may develop indistinct tubercles on the dorsal surface of pereonites 1 and 3.

Size. Adults to 13.2 mm.

Remarks. *Natatolana amplocula* is most similar to *N. albicaudata* (see remarks for that species) and *N. curta*. *Natatolana curta* was described from a single specimen and has not been subsequently collected. The uropod endopod is less rounded in the holotype of *N. amplocula*, than in the holotype of *N. curta* but the specimen of *N. curta* is larger and may have had the distal lateral margins somewhat worn down. Other differences of the holotype of *N. curta* to that of *N. amplocula* follow with the state for *N. amplocula* in parentheses: interocular furrow incomplete (complete); dorsal posterolateral margin of pleonite 2 produced posterior to ventral posterolateral margin (subequal), 11 robust setae on the pleotelson margin (six); indistinct tubercles on the dorsal surface of pereonites 1 and 3 (absent—but this appears to be a sexually dimorphic character found only in mature males and the holotype of *N. amplocula* is female).

The specimens reported here are only tentatively identified as *Natatolana amplocula* because of the difficulties in differentiating this species as noted above. None of the specimens examined were as large as the holotype of *N. curta* and none had the uropod endopod as strongly rounded. In other respects, all of the material examined appeared to be intermediate between *N. amplocula* and *N. curta* because: all specimens have a complete interocular furrow; the number of robust setae on the pleotelson varies between 6–12; and the dorsal posterolateral margin of pleonite 2 is produced posterior to the ventral posterolateral margin. Furthermore, the holotype of *N. curta* is a male and has indistinct tubercles on the dorsal surface of pereonites 1 and 3. In a number of samples examined here, similar tubercles were found on male specimens but never females. Because of the limited type material of *N. amplocula* the significance of these tubercles is unclear.

Distribution. Philippines, Indonesia, northwestern and northeastern Australia, southern Pacific Ocean as far west as the Kermadec Islands and as far south as Taupo Seamount. Recorded from surface plankton to a depth of 441 m.

Natatolana angula Bruce, 1986

Natatolana angula Bruce, 1986: 106, fig. 73.–Springthorpe & Lowry, 1994: 37.–Brusca *et al.*, 1995: 79.–Keable, 1997: 255, fig. 1e.–Bruce *et al.*, 2002: 149.
Natatolana cf. *angula*.–Keable, 1995: 43.

Type material. Holotype: ♂, QM W9795. Paratypes: QM W9797-9800; AM P32380 (examined); USNM; NTM. • Type locality: Halifax Bay, Townsville, Queensland, Australia, 19°08'S 146°19'E.

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4× as long as body, reaching to between the posterior of pereonite 3 and 4 (pereonite 2 according to Bruce (1986), however, in one paratype from AM P32380 it reaches to the posterior of pereonite 3 and in the other it reaches to one third of the way along pereonite 4). *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.76× basal width; anterodorsal

depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle or convex (on paratypes the posterior margin appears straight); apex not produced, lateral margins converging smoothly to a point; with 8–12 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.58× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod; margins very slightly curved laterally or straight; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Size. Adults to 13.5 mm.

Remarks. Identification, distribution, ecology and character variation for *Natatolana angula* is discussed by Keable (1997) who also re-illustrated the uropod.

Distribution and ecology. Australia: northern Western Australia, Darwin (Northern Territory), northern Queensland south to Gladstone. Hayward *et al.* (2001) report "*Notatolana* [sic] '*angula*'" from New Zealand, this requires confirmation. Intertidal to 83 m depth. Scavenger.

Natatolana anophthalma (Kussakin & Vasina, 1982)

Cirolana anophthalma Kussakin & Vasina, 1982a: 263, figs. 3, 4.–1982b: 329, 336.

Natatolana anophthalma.–Bruce, 1986: 222.–?Kensley, 1989: 149.–Brusca *et al.*, 1995: 79.

Natatolana anopthalma.–Kensley, 2001: 230 [*lapsus*].

Type material. Holotype: ♂, 21.2 mm, ZIAS No. 1/71 226 (not examined). • Type locality: Kerguelen Islands, 47°57'S 69°02'E, 175 m.

Material examined. St. Paul and Amsterdam Islands, southern Indian Ocean, manca, USNM 252158 38°24.4'S 77°34.8'E, 1430–1600 m, previously determined by Kensley (1989).

Diagnosis. Details of the interocular furrow, labrum, coxa 2, number of robust setae on the pleotelson, setation and size of the pereopod articles, penes, and setation of the uropod exopod are unknown. *Eyes*: vestigial or absent. *Antenna*: c. 0.3× as long as body, reaching to at least the posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; RS present (not mentioned in original description but apparent in illustration). *Pereopod 7*: basis narrow. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; margins strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded (described as rounded but appears truncate in the original illustration). *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Sexual dimorphism. Unknown.

Size. Holotype ♂ 21.2 mm, manca recorded by Kensley (1989) 8 mm.

Remarks. An attempt to borrow the holotype of *Natatolana anophthalma* from the Zoological Institute of the Academy of Science, St. Petersburg, was unsuccessful. Other than the type material, the only record of this species is that of Kensley (1989) who recorded two specimens from St. Paul and Amsterdam Islands. Only one of these specimens, a manca, is now available. This specimen was examined but, because it is a juvenile, characters such as the shape of the appendix masculina and basis of pereopod 7 could not be observed and the identification of the species is considered here to be doubtful. Examination of the type material is needed to distinguish this species from a number of similar species such as *N. californiensis*.

Distribution. Kerguelen Islands (type locality, 175 m); possibly also occurring at St. Paul and Amsterdam Islands, southern Indian Ocean (1430–1600 m).

Natatolana aotearoa n.sp.

Figs. 5–6

Type material. HOLOTYPE: ♂, 19 mm, NIWA 18748. PARATYPES: all from **New Zealand**: ♀, ZMUC CRU108, Milford Sound, 44°34'S 167°48'E, mud with sand and clay, 136 m, *Galathea* Station 619, 19 Jan. 1952; ♀, 5♂♂, NMNZ 9203, Akaroa Harbour entrance, c. 44°S 173°E, black mud, 13–15 m, RV Acheron, 20 Feb. 1979, BS 782; 3♀♀, NMNZ 9204, northwest of Manawatu River, 40°22.5'S 174°59.5'E, 86 m, RV Acheron, 2 Mar. 1976, BS 495. Series from off the west coast of the South Island, dredge-anchor box, P.K. Probert: manca, NIWA 18750, 42°48.5'S 169°53.5'E, silt-clay, 520 m, 20 Feb. 1982; 2 mancas, NIWA 18751, 41°25.5'S 171°10.3'E, silt-clay, 172 m, 25 Feb. 1982; manca, NIWA 18752, 42°24.5'S 170°57.5'E, sand-silt-clay, 133 m, 28 Feb. 1982; ♀, manca, NIWA 18753, 42°23.4'S 170°53.6'E, sand-silt-clay, 167 m, 4 Mar. 1982; ♂, 2 mancas, NIWA 18754, 42°57.7'S 170°12.4'E, silt-clay, 109 m, 18 Feb. 1982; ♂, NIWA 18756, 41°33.4'S 171°25'E, sand-silt-clay, 140 m, 25 Feb. 1982; ♀, NIWA 18755, 42°25.7'S 171°01.8'E, sand-silt-clay, 87 m, 28 Feb. 1982. • Type locality: off west coast of South Island, New Zealand, 41°25.5'S 171°10.3'E, silt-clay, 172 m [dredge-anchor box, P.K. Probert, 25 Feb. 1982].

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, forming a ridge that extends across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.4× as long as body, reaching to half way along pereonite 4. *Coxal plates*: furrows variously developed, strongly developed on coxae 2–3, absent on coxae 4–6, moderately developed on coxa 7. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.86× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 6 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: ischium anterodistal angle produced, but not as produced as on pereopods 1 and 2, similar to pereopod 4. Propodus with 1 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1.01× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.8× the length of the endopod.

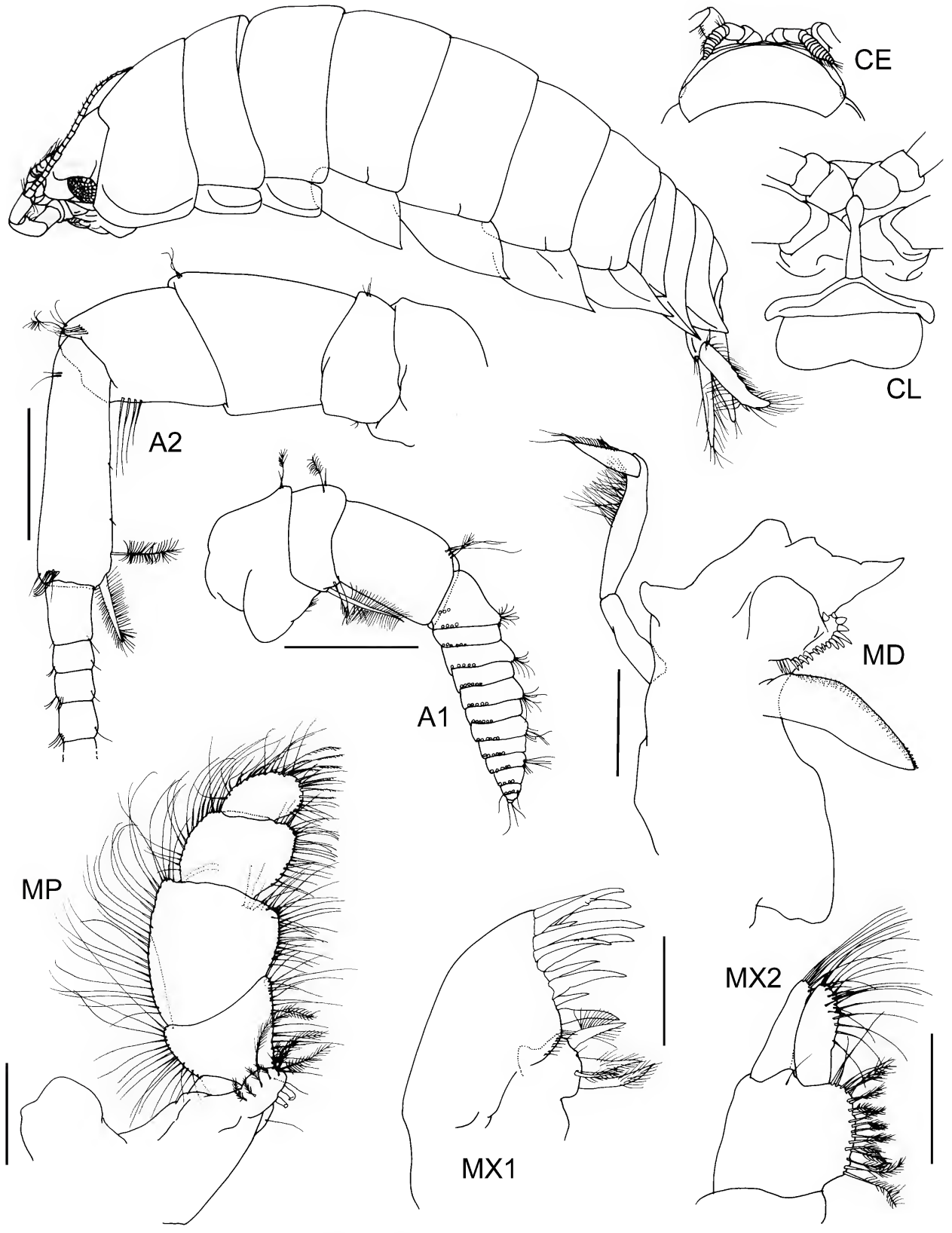

Fig. 5. *Natatolana aotearoa*, n.sp., holotype. Scales = 0.5 mm.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.6× width. Colour cream in alcohol. Chromatophores absent. *Eyes*: with 7 ommatidia in horizontal diameter; with 7 ommatidia in vertical diameter; round; colour white in alcohol. *Frontal lamina*: length c. 4.5× basal width; apex expanded, anterior margin rounded. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 13-articulate. *Antenna*: peduncular article 4 with 4 SS on posterolateral margin, 8 SS and 1 penicillate seta at anterodistal angle; article 5 with 2 pappose setae at posterodistal angle, 6 SS at anterodistal angle. Flagellum 27-

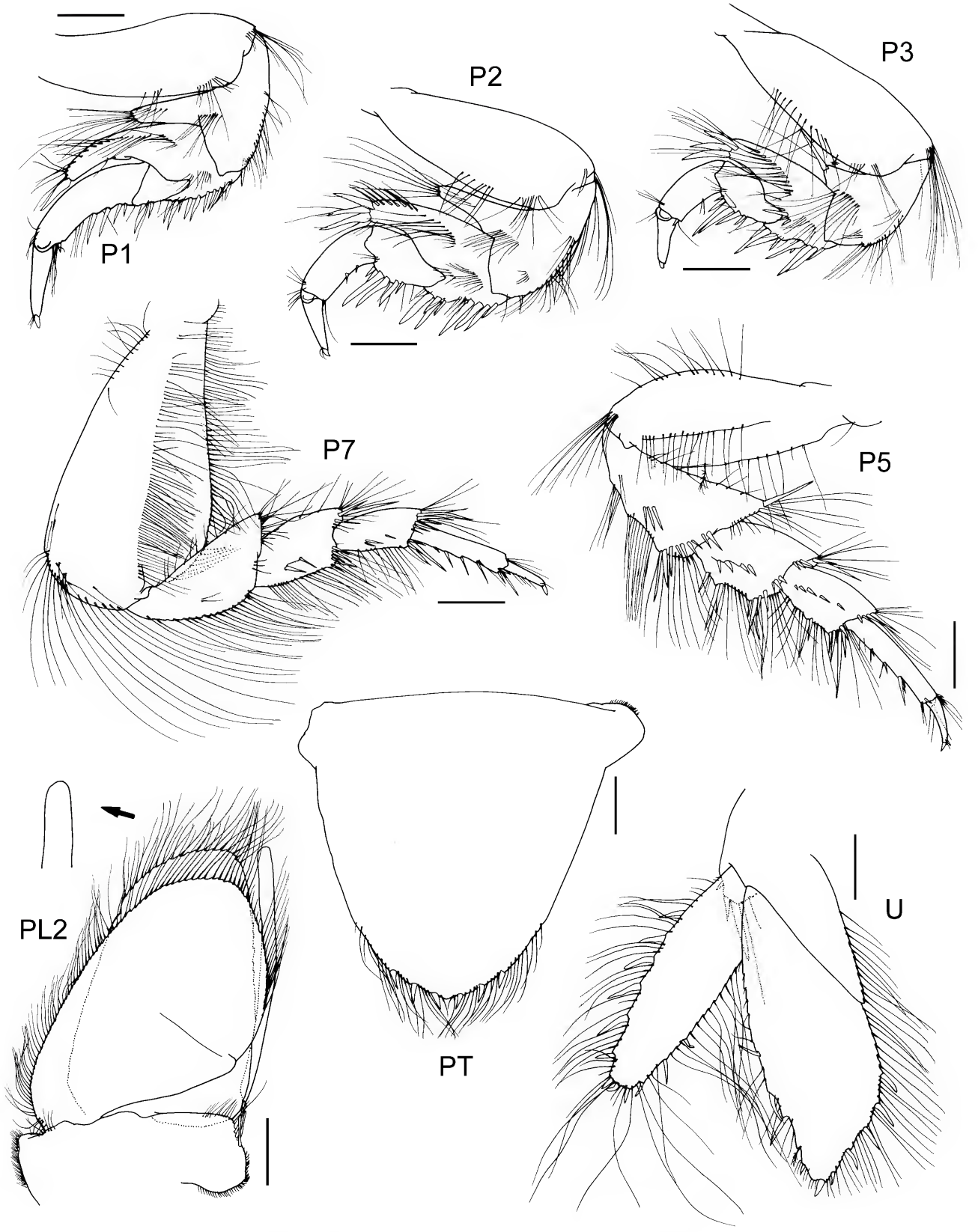

Fig. 6. *Natatolana aotearoa*, n.sp., holotype. Scales = 0.5 mm.

articulate. *Mandible*: setal row with 19 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 6 SS; medial lobe with 5 SS and 17 PS; middle lobe with 20 SS. *Maxilliped*: endite with 2 coupling hooks, and 9 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–7; pereonite 1 longest, 4–6 subequal and longer than 2–3 and 7 which are subequal. *Coxae*: pereonite 1, coxa 2 with rounded posteroventral corners, coxa 3 with a square posteroventral corner, coxae 4–7 with increasingly produced, acute posteroventral corners. *Pleonites*:

1–5 visible but 1 almost completely concealed along dorsal margin by pereonite 7. *Pleonite 2*: dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin. *Pereopod 7*: basis anterior margin sinuate; medial carina with PS along entire length; posterior margin convex, PS present. Ischium anterior margin with SS; posterior margin without RS, PS present. Merus anterior margin with SS; posterior margin without RS (2 submarginally), SS present. Carpus posterior margin without RS (3 submarginally), SS present. Propodus longer than carpus; posterior margin with 6 RS, SS present. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly sinuate, with 4 RS, PS on distal three-quarters. Exopod medial margin convex, with 4 RS, PS on distal three-quarters; apex acute, with 2 RS; lateral margin convex, with 6 RS, PS along entire length.

Size. Adults to c. 20 mm.

Etymology. From the Māori for New Zealand, meaning land of the long white cloud or long bright land, in reference to the species distribution.

Remarks. *Natatolana aotearoa* is most similar to *N. thurar*. In both of these species the eyes have indistinct ommatidia that lack pigment, the interocular furrow is developed into a ridge and the posterodorsal margin of pleonite 4 is concave with the apex developed into a narrow acute point. *Natatolana aotearoa*, however, differs in having the ischium of pereopods 1–2 more produced, with distinctly concave anterodistal margins, and in having the ischium of pereopod 3 less produced. The apex of the frontal lamina is also less acute and the lateral margins not parallel as in *N. thurar*.

Distribution. New Zealand; known only from the west coast. At depths of 13–520 m.

Natatolana arcicauda (Holdich, Harrison & Bruce, 1981)

Cirolana arcicauda Holdich *et al.*, 1981: 563, fig. 14.
Natatolana lurur Bruce, 1986: 89, fig. 61.–Brusca *et al.*, 1995: 80.–Kensley, 2001: 230.
Cirolana woodjonesi.–Hale, 1940: 288 (part) [mis-identification, not *N. woodjonesi* (Hale, 1924)].
Natatolana arcicauda.–Bruce, 1981: 958.–1986: 89, fig. 59.–Brusca *et al.*, 1995: 79.–Bruce *et al.*, 2002: 149.

Type material of *N. arcicauda*. Holotype: female, 11.3 mm, QM W6335 (examined). Paratypes: ♂, 10.5 mm, QM W6336 (examined); ♂, but institution where deposited not stated, possibly in Nottingham University. • Type locality of *N. arcicauda*: Cleveland Bay, Townsville, Queensland, Australia [19°13'S 146°55'E].

Type material of *N. lurur*. Holotype: ♀, 15.8 mm, WAM 46-80. Paratype: WAM 20-80. All examined. • Type locality of *N. lurur*: northwest of Bluff Point, Geraldton, WA, Australia, 27°40'S 113°03'E, 150 m.

Material examined. **Queensland**: 6, AM P47294, off Flynn Reef, 16°41.32'S 146°18.26'E, 100 m, 7–8 Jun. 1993, SEAS QLD-937; 5, AM P47295, due east of Mooloolaba, 26°39.13'S 153°18.88'E, 51 m, 2–3 Aug. 1994, SEAS QLD-1122. **Western Australia**: 3♂♂, 5♀♀, AM P47709, off Kimberley Plateau, c. 16°8.86'S 123°27.76'E, baited trap, 20 m, F. Wells, 1994, stn 20.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon, or moderately developed, distinct but not extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.36× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed, strongly developed on coxae 2, 3 and 7, absent on coxae 4, 5 and 6, or weakly developed on coxae 2–3 and strongly developed on coxa 7, or moderately developed on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.75× basal width; anterodorsal depression absent; anterolateral margins convex, or almost straight and angling posteriorly toward the midline; posterolateral margins broadly rounded, or straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex not produced, lateral margins converging smoothly to a point; with 8–10 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis narrow, width 0.43–0.46× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.83× the length of the endopod.

Variation. The holotype of *Natatolana arcicauda* has eight robust setae on the margin of the pleotelson and the holotype of *N. lurur* has 10 robust setae on this margin. Specimens from Kimberley Plateau on the northwest coast of Australia (AM P47709) and Flynn Reef off the northeast coast (AM P47294) have a range of eight to 10 robust setae on the pleotelson. All of the specimens examined, other than the holotype of *N. arcicauda*, have an angular pleotelson as described for this species by Bruce (1986). Specimens from east of Mooloolaba on the northeast Australian coast (AM P47295) have a complete interocular furrow and indistinct coxal furrows on all coxae.

Size. Adults 11.3–18.9 mm.

Remarks. Bruce (1986) discussed the differences between *Natatolana lurur* and *N. thurar*. Differences between *N. lurur* and *N. arcicauda*, however, were not discussed. Comparison of the original descriptions of *N. arcicauda* and *N. lurur*, and the additional description of *N. arcicauda* by Bruce (1986), indicate six possible significant distinctions between the two species. These are differences in the shape of the frontal lamina, development of the interocular furrow, length of the antennae combined with the number of articles in the antennal flagellum, the distribution of the coxal furrows, the shape of the pleotelson and the number of robust setae on the margins of the pleotelson. Examination of the holotypes of both species and of additional material, however, indicates that these differences are not profound. The reasons for this conclusion are discussed below.

While the frontal lamina of *Natatolana arcicauda* has been illustrated as having an angular apex (Bruce, 1986) it is actually rounded as in the type material of *N. lurur*. Similarly, the length of the antennae in the type material of *N. lurur* is incorrectly described. Instead of extending to the posterior of pereonite 2 and having 28 articles in the flagella, the antennae extend to the posterior of pereonite 3 and have between 21 and 25 articles in the flagella, (23 articles in *N. arcicauda*). Furthermore, although the furrows on coxae 2 and 3 of the holotype of *N. arcicauda* are not as

well developed as those in the type material of *N. lurur*, they are still present. The interocular furrow is incomplete in the type material of *N. arcicauda* and complete in that of *N. lurur*. Comparison with additional material from near the type locality of *N. arcicauda* (AM P47294–5), however, suggests this is a variable character. Similarly, differences in the number of robust setae on the margins of the pleotelson appear to represent intra-specific rather than inter-specific variation. The margins of the pleotelson of the holotype of *N. arcicauda* appear worn and damaged and Bruce (1986) has indicated that the shape of the pleotelson is variable and can resemble that described for *N. lurur*.

Additionally, the general agreement in alternative characters, such as the shape of the coxae and pleonites, and the shape and setation of the pereopods and uropods, suggest that the two nominal taxa are conspecific. Accordingly, *Natatolana lurur* is recognized as a junior subjective synonym of *N. arcicauda* as reported in Bruce *et al.* (2002).

Distribution and ecology. Australia, off Geraldton and Kimberley Plateau (Western Australia) and off Cairns to Mooloolaba (Queensland). At depths of 2.7–150 m. Scavenger.

Natatolana arrama Bruce, 1986

Natatolana arrama Bruce, 1986: 108, fig. 74.–Springthorpe & Lowry, 1994: 38.–Brusca *et al.*, 1995: 79.–Bruce *et al.*, 2002: 149.

Type material. Holotype: ♀, 11.1 mm, AM P30363. Paratype: AM P30362. All examined. • Type locality: south of Portland, Victoria, Australia, 38°52'S 141°50'E, 77 m.

Material examined. **New South Wales**: 21, AM P47468, east of Coffs Harbour, 30°17.49'S 153°13.90'E, 45.4 m, 11–12 Aug. 1993, SEAS NSW-873; 30, AM P47469, off Providential Head, 34°44'S 150°39'E, baited trap, 45–50 m, S. Keable, A. Parker & J. Lowry, 14–15 Jan. 1991, PIO-107; 502, AM P44317, off Wollongong, 34°26.54'S 150°57.98'E, 50 m, 28 Mar. 1994, SEAS NSW-956. **Tasmania**: 175, AM P47470, about 800 m east of Point Geographe, Freycinet Peninsula, 42°17'S 148°18.8'E, baited trap, 45 m, J.K. Lowry & S.J. Keable, 30 April–1 May 1991, TAS-337.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.24× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.93× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 4 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.68× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins straight or very slightly curved laterally; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.82× the length of the endopod; lateral margin without RS.

Size. Adults to c. 12.6 mm.

Remarks. This is the first record of a male specimen of *Natatolana arrama*. Bruce (1986) appears to have illustrated and described pereopod 6 of this species rather than pereopod 7 as stated. The anterior margin of the basis of pereopod 7 is sinuate and the posterior margin convex—not both strongly convex as originally described.

Using the key provided by Bruce (1986) this species can only be reached if it is assumed in couplet 21 that it has six or more robust setae on the pleotelson, whereas it only has four. *Natatolana arrama* is most readily identified by the lack of robust setae on the uropod exopod lateral margin combined with straight lateral margins of the frontal lamina that converge anteriorly to form an unexpanded and acute apex.

Distribution and ecology. Australia: central New South Wales, off the east coast of Tasmania, Bass Strait (off Portland, Victoria, and Eucla, South Australia). At depths of 45–77 m. Scavenger.

Natatolana boko Bruce, 1986

Natatolana boko Bruce, 1986: 59, fig. 35, 36.–Springthorpe & Lowry, 1994: 40.–Brusca *et al.*, 1995: 79.–Bruce *et al.*, 2002: 149.

Type material. Holotype: ♂, 5.2 mm, AM P32173. Paratype: AM P30382. All examined. • Type locality: east of Lady Musgrave Island, Queensland, Australia, 23°44'S 152°49'E, 357–384 m.

Material examined. **Tasmania**: 15, NMV J18419-21, all off Freycinet Peninsula, 41°57.5'–42°2.2'S 148°37.7'–148°38.7'E, sled, coarse shell or shelly sand, 400–800 m, M.F. Gomon *et al.*, 27 Jul. 1986.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, extending across the cephalon (described by Bruce (1986) as submarginal furrow); smoothly convex. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.25–0.3× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows completely absent on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.67× basal width; anterodorsal depression absent (although described by Bruce (1986) as having a depression, this is not distinct and abrupt as in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins concave; apex not produced, lateral margins converging smoothly to a point; RS absent. *Pereopod 2*: propodus with 0–2 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.54× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae on proximal half. *Penes*: present (although the vas deferens are described as opening flush to the sternite surface by Bruce (1986), distinct penial processes are evident in the type material and other material examined). *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1.03× length of endopod; slender; margins very slightly curved laterally; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.6× the length of the endopod; lateral margin without RS.

Size. Adults to c. 5.2 mm.

Remarks. *Natatolana boko* can be readily distinguished from other species by the sinuate lateral margins of the pleotelson and uropod endopod, both of which also lack robust setae.

Distribution. Australia: off Lady Musgrave Island, Queensland; Freycinet Peninsula, Tasmania. At depths of 357–800 m.

Natatolana borealis (Liljeborg, 1851)

Synonymy in Keable & Bruce, 1997: 659, figs. 1–4.

Type material. Syntypes: deposition of the original material was not indicated, 3 ♂♂, 5 ?♀♀ in the Zoological Museum, Lund University, Sweden, probably represent at least part of the original type series examined by Liljeborg (Keable & Bruce, 1997). All examined. • Type locality: Kristiansund [as Christiansund, c. 63°23'N 7°45'E] and Bergen [c. 60°23'N 5°20'E], Norway.

Material examined. Listed by Keable & Bruce (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.4× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows variously developed, faint and incomplete on coxae 2 and 3 only. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.96× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 6–8 RS. *Pereopod 2*: propodus with 4–6 RS on palm (4 large and 2 small). *Pereopod 3*: propodus with 3 RS on palm. *Pereopod 7*: basis broad, width 0.57× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.87× length of endopod; margins straight or bent slightly medially; slender; apex not at angle to adjacent margins, with lateral projection forming a Y-shape with acute apex. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Variation. In smaller males (e.g., 22 mm) the appendix masculina is shorter (e.g., 0.81× endopod) and the Y shaped process on the appendix masculina apex may be absent or only partially developed (Keable & Bruce, 1997).

Size. Adults to c. 33 mm.

Remarks. Keable & Bruce (1997) redescribe *Natatolana borealis* and discuss its identification and character variation. This species can be readily recognized by the shape and setation of the uropods and pleotelson, and by the distinctive shape of the appendix masculina of adult males.

The material of *Natatolana borealis* reported from South Africa by Kensley (1975, 1978) is not *N. borealis*. Kensley (1975) noted the South African specimens have coxae with sinuate posterior margins, and a small notch at postero-ventral corner where an acute coxal point is produced. Kensley suggested that this was a variation that may be due to the immaturity of the specimens. This does not seem to be the case, juvenile *Natatolana* usually resemble the adult very closely in these features (personal observation) and the coxae of smaller specimens identified by Keable & Bruce (1997), as *N. borealis*, are similar to those of the adults. Also, one of the specimens reported by Kensley (1975) (SAM A-13556) has an apparently fully developed basis of pereopod 7 attached to the body and can therefore be considered to have reached adult size. A unusual feature of the South African specimens is that the carpus of pereopods 4–5 [figured as pereopod 6 by Kensley (1975)] is greatly elongated (c. 2 times as long as the merus and 1.5 times as long as the propodus). This is a unique character within *Natatolana* and indicates that these specimens represent an undescribed species. Unfortunately, the material is not in good enough condition to describe.

Distribution and ecology. Disjunct North Atlantic records—primarily recorded from northeastern Atlantic coasts between 70° and 10°N, westwards to about 22°W but also recorded from off South Carolina, USA (Keable & Bruce, 1997; Johansen & Brattegard, 1998). At depths of 5–1478 m with the depth range varying with locality (Keable & Bruce, 1997; Johansen & Brattegard, 1998).

Natatolana borealis is well documented as a scavenger, feeding on dead and dying fish (Keable & Bruce, 1997). Ecological and physiological studies reporting this species, subsequent to those summarized by Keable & Bruce (1997), include Johansen (1999, 2000a, 2000b), Johansen & Brattegard (1998), Kaïm-Malka (1997), Kaïm-Malka *et al.* (1998), Bozzano & Sarda (2002) and Castro *et al.* (2005).

Natatolana bowmani Bruce, 1986

Natatolana bowmani Bruce, 1986: 60, fig. 37.–Springthorpe & Lowry, 1994: 40.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♂, 13.8 mm, AM P33555. Paratypes: AM P31573–P31576, P31905. All examined. • Type locality: east of Port Jackson, NSW, Australia, 33°36'S 152°05'E, 1090–1125 m.

Material examined. **New South Wales**: 5, AM P47296, northeast of Coffs Harbour, 30°10.94'S 153°32.27'E, 1000 m, 11–12 Aug. 1993, SEAS NSW-862; 210, AM P44364, off Wollongong, 34°33.41'S 151°21.35'E, 1000 m, 6–7 May 1993, SEAS NSW-788. **Tasmania**: 29, AM P47297, east of Fortescue Bay, 43°08.96'S 145°15.36'E, 1000 m, 8–9 April 1994, SEAS TAS-403.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel, or lateral margins concave but not medially constricted, broadening anteriorly. *Antenna*: c. 0.38× as long as body, reaching to slightly beyond the posterior of pereonite 3 to half way along pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point, or apex slightly rounded. *Pleotelson*: broad, length 0.82× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point, or produced into a small point; with 4–8 RS. *Pereopod 2*: propodus with 1 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis narrow, width 0.38× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on distal third. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.03× length of endopod; slender; margins very slightly curved laterally; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.8× the length of the endopod.

Sexual dimorphism. Females have the pereon slightly broader than males.

Size. Mancas to 5.8 mm, males to 13.8 mm; females to 14.0 mm.

Remarks. Examination of the holotype of *Natatolana bowmani* indicates that the anterior apex of the frontal lamina is more angled than illustrated by Bruce (1986). The

margins of the pleotelson of the holotype and some paratype material appear worn and damaged. On some of the paratypes and other specimens examined there are eight robust setae on the posterolateral margins of the pleotelson, not four as described by Bruce (1986). The vestigial eyes, presence of penes, shape of pleonite 4 and morphology of the appendix masculina are the most useful characters in differentiating *N. bowmani* from similar species.

Distribution and ecology. Australia: between Coffs Harbour and Port Kembla, New South Wales; and east coast of Tasmania. At depths of 880–1200 m. Scavenger.

Natatolana brucei n.sp.

Figs. 7–8

Type material. HOLOTYPE: ♂, 16.0 mm, AM P47185. PARATYPES: 116, AM P38675; ♂, ♀ at BMNH, USNM, ZMUC. • Type locality: off Grotto Point, Port Jackson, NSW, Australia, 33°49.2'S 151°15.75'E, [baited trap, unknown substrate, probably sediment], 10 m, [S. Keable, J. Lowry & D. Townsend, 16–17 Jul. 1988, Site 37].

Additional material. **New South Wales**: 9, AM P47199, off Grotto Point, Port Jackson, 33°49.05'S 151°15.8'E, baited trap on sediment, 15 m, S. Keable & J. Lowry, 8–9 May 1988, site 13; series from south of Sydney, Australian Museum/The Ecology Lab Pty. Ltd. *Pioneer* Consultation Project 1991, off Providential Head, 34°44'S 150°39'E, baited traps, S. Keable, A. Parker & J. Lowry on MV *Krista*, 14–15 Jan. 1991: AM P47202–47207; ♀, 25–30 m, PIO-101; ♂, 2 mancas, 25–30 m, PI0-103; ♀, 33 m, PIO-116; off Bate Bay/Port Hacking, 34°07.00'S 151°10.00'E: 4, 25–30 m, S2R1 shallow; ♂, ♀, manca, 25–30 m, S2R2 shallow; ♂, 35–40 m, S2R2 medium; series from Twofold Bay, baited trap, J. Lowry & S. Keable, 27–29 Nov. 1988: 9, AM P47200, between Whale Spit and Mungora Point, 37°5.7'S 149°53.1'E, unknown substrate, probably sediment, 8 m, NSW-381; 2, AM P47201, between Lookout Point and Seahorse Shoals, 37°5.6'S 149°56.6'E, unknown substrate—probably sediment, 30 m, NSW-392.

Diagnosis. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.3× as long as body, reaching to just beyond posterior of pereonite 3. *Coxal plates*: furrows variously developed, strong and complete on coxae 2–3, 7, indistinct and incomplete on coxae 4–6. *Pleonite 4*: apex slightly rounded. *Pleotelson*: narrow, length 1.14× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins concave; apex produced into a large point; with 6 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.61× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal half. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.04× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 3.3× width. Colour cream in alcohol. Chromatophores absent. *Eyes*: with 7 ommatidia in horizontal diameter; with 8 ommatidia in vertical diameter; ovate; colour tan in alcohol. *Frontal lamina*: length c. 6.8× basal width; apex not expanded, anterior margin rounded. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta (broken); article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 12-articulate. *Antenna*: peduncular article 4 with 2 SS and 1 penicillate seta medially on posterolateral margin, 2 SS at posterodistal angle, 2 SS at anterodistal angle; article 5 with 1 pappose and 1 PS at posterodistal angle, 3 SS and 1 penicillate seta at anterodistal angle. Flagellum 22-articulate. *Mandible*: setal row with 14 RS. *Maxillule*: medial lobe with 3 large robust pappose setae and 3 SS; lateral lobe with 12 RS on distal surface. *Maxilla*: lateral lobe with 6 SS; medial lobe with 5 SS and 9 PS; middle lobe with 12 SS. *Maxilliped*: endite with 2 coupling hooks, 1 SS and 6 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–6; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: pereonite 1 and coxae 2–3 with rounded posteroventral corners, coxae 5–7 with sinuate posterior margins formed into moderately large coxal points. *Pleonites*: 1–5 visible but 1 almost completely concealed along dorsal margin by pereonite 7. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin sinuate; medial carina with PS and SS present (plumose setae on proximal third, slender setae on distal third); posterior margin convex, PS present. Ischium anterior margin with SS; posterior margin with 1 RS (submarginal), PS present. Merus posterior margin with 7 RS (and 4 submarginally), SS present. Carpus posterior margin with 6 RS (2 submarginally), SS absent. Propodus longer than carpus; posterior margin with 7 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 4 RS, PS along entire length; apex with 2 RS; lateral margin slightly sinuate, with 3 RS and 1 penicillate seta, PS on distal three-quarters. Exopod medial margin convex, with 2 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 7 RS, PS along entire length.

Size. Adults to c. 16 mm.

Etymology. Named after Dr Niel Bruce, in recognition of the help he has given me with this study.

Remarks. *Natatolana brucei* appears to be very similar to *N. pallidocula* but differs in having a round eye with fewer ommatidia, a rounded posteroventral margin on coxa 3, a antennal flagellum with more articles, a longer appendix masculina and a broader pereopod 7.

Distribution and ecology. Australia: New South Wales within Port Jackson and off the coast south of Port Jackson; Twofold Bay. At depths of 8–40 m. Scavenger.

Natatolana bulba Bruce, 1986

Natatolana bulba Bruce, 1986: 108, fig. 75.–Springthorpe & Lowry, 1994: 41.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♂, 9.5 mm, AM P32174. Paratypes: AM E4843. All examined. • Type locality: off North West Island, Capricorn Group, Southern Great Barrier Reef, Queensland, Australia, 23°17.5'S 151°42'E, 40 m.

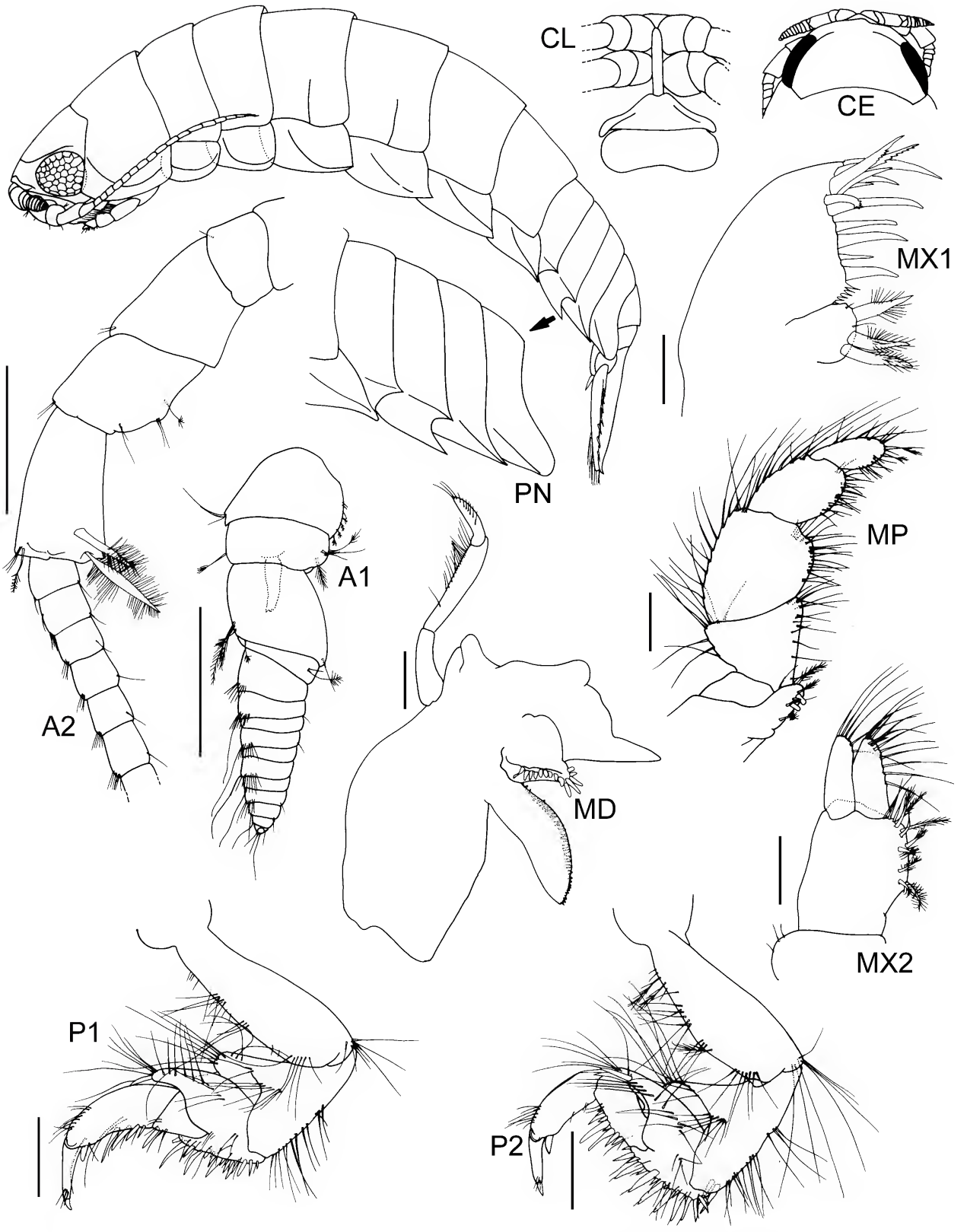

Fig. 7. *Natatolana brucei*, n.sp., holotype. Scales for A1, A2, P1, P2 = 0.5 mm. Scales for MD, MP, MX1, MX2 = 0.2 mm.

Material examined. **Queensland**: series from off Flynn Reef: ♂, AM P47632, 16°41.32'S 146°18.26'E, 100 m, 6–7 Jun. 1993, SEAS QLD-920; 4, AM P47633, 16°40.82'S 146°18.81'E, 200 m, 7–8 Jun. 1993, SEAS QLD-940; series from off East Fitzroy Reef; 22, AM P47634, 23°32.53'S 152°16.45'E, 105 m, 16–17 Jun. 1993, SEAS QLD-956; 3, AM P47635, 23°30.46'S 152°21.32'E, 300 m, 16–17 Jun. 1993, SEAS QLD-960; 9, AM P47636, due east of Mooloolaba, 26°39.13'S 153°18.88'E, 51 m, 2–3 Aug. 1994, SEAS QLD-1122. **New South Wales**: series from northeast and east of Coffs Harbour; 21, AM P47637, 30°15.86'S 153°21.90'E, 92.7 m, 11–12 Aug. 1993, SEAS NSW-870; 6, AM P47638, 30°17.49'S 153°13.90'E, 45.4 m, 11–12 Aug. 1993,

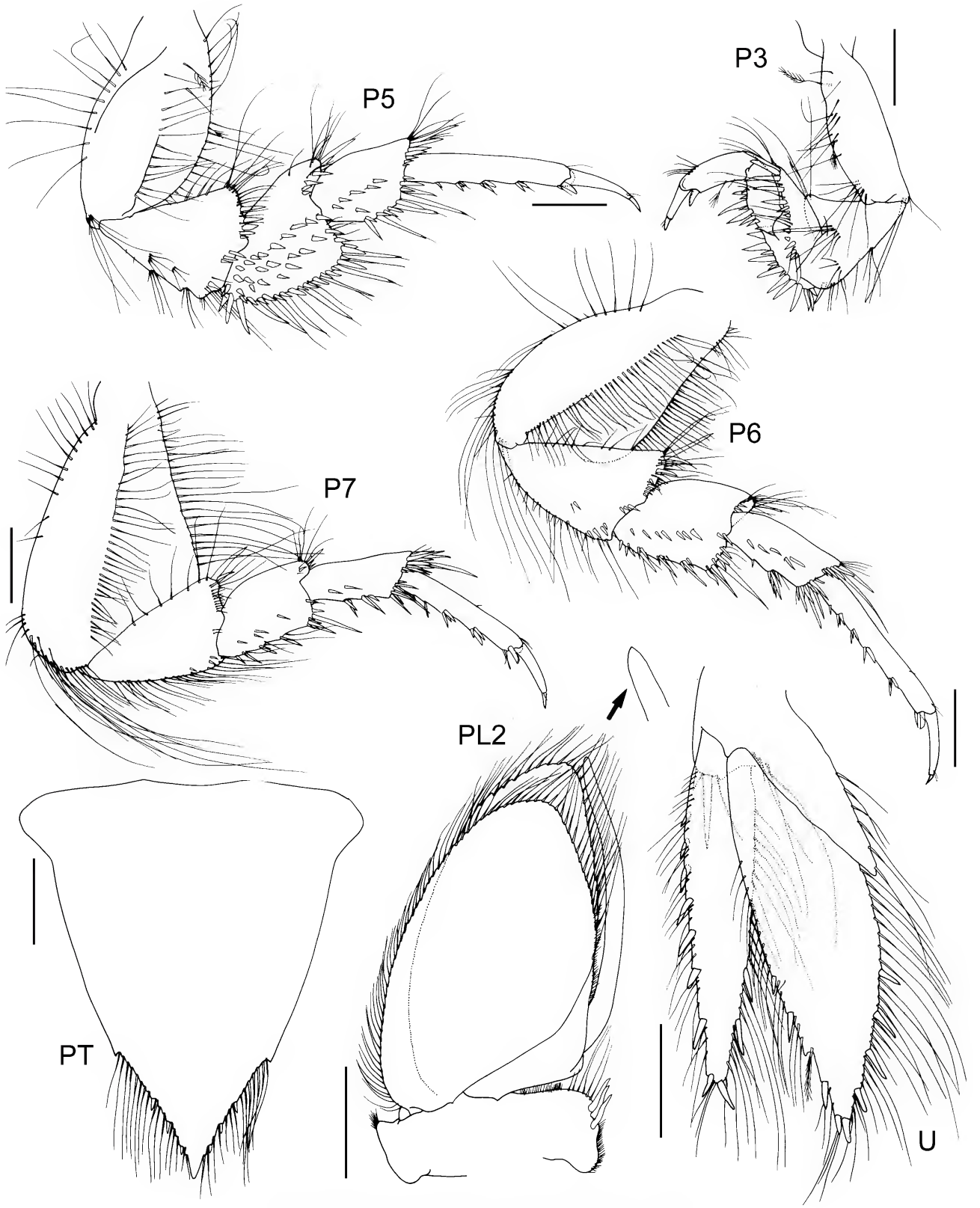

Fig. 8. *Natatolana brucei* n.sp., holotype. Scales = 0.5 mm.

SEAS NSW-873; 62, AM P47639, 30°15.75'S 153°21.98'E, 98 m, 12–13 Aug. 1993, SEAS NSW-885; 19, AM P47641, 30°12.97'S 153°29.23'E, 400 m, 8–9 Sep. 1994, SEAS NSW-994; many, AM P47640, 1.7 km east of Ramsgate, Botany Bay, 33°59.1'S 151°9.95'E, baited trap, 5 m, S. Keable & R. Springthorpe, 7–8 April 1992, FACSCAV-30; 6, AM P47642, Parriwi Point, Port Jackson, 33°48.5'S 151°14.8'E, baited trap, sediment, 8 m, S. Keable & J. Lowry, 23–24 Sep. 1988, site 49; 66, AM P47643, off Wollongong, 34°32.53'S 151°17.07'E, 400 m, 6–7 May 1993, SEAS NSW-787. **Tasmania**: series from east of Fortescue Bay; 25, AM P47645, 43°07.77'S 145°59.47'E, baited trap, 50 m, 17–18 April 1993, SEAS TAS-368; 8, AM P47648, 43°08.96'S 145°15.36'E, 1000 m, 17–18 April 1993, SEAS TAS-383; 10, AM P38833, 43°07.77'S 145°59.47'E, 50 m, 8–9 April

1994, SEAS TAS-386; 56, AM P47647, about 80 m outside Hannants Bight, north side of Cape Sorell, 42°11.5'S 145°11'E, sand and detritus, 18 m, J. Lowry & S. Keable, 26–27 April 1991, TAS-277.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon or well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.25–0.3× as long as body, reaching to between the posterior of pereonite 2 and 3. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.9 basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 4–6 RS (4 in types). *Pereopods 1–6*: males with RS on the merus of pereopods 1–3, and carpus of pereopods 4–6, shorter than the propodus. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.6× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod; margins very slightly curved laterally; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod short, 0.75× the length of the endopod; lateral margin without RS.

Variation. All material noted here is tentatively identified as *Natatolana bulba*. Some of the material examined from Queensland (Flynn Reef: AM P47632, AM P47633; Fitzroy Reef: AM P47635), New South Wales (Botany Bay: AM P47641; Wollongong: AM P47643) and eastern Tasmania (AM P47648) have a narrower apex to the uropod endopod than the type specimens. Of these, those from Fitzroy Reef, Queensland (AM P47635) and Botany Bay, New South Wales (AM P47641) also have a complete interocular furrow. Specimens from Wollongong, New South Wales (AM P47643), however, have a narrow apex to the uropod endopod and a complete or an incomplete interocular furrow. Specimens from eastern Tasmania (AM P38833) have the apex of the uropod endopod intermediate between those of the type specimens and those from Wollongong, New South Wales (AM P47643). Specimens from New South Wales (Port Jackson: AM P47642), eastern Tasmania (AM P47645) and western Tasmania (AM P47647) have the antennae reaching to the posterior of pereonite 2, not pereonite 3 as in the types. The sample from Mooloolaba, Queensland (AM P47636), however, contains specimens with antennae that reach to the posterior of pereonite 2 and also some in which the antennae reach to the posterior of pereonite 3. In the material from western Tasmania (AM P47647) there are a few specimens with five or six robust setae on the pleotelson rather than the usual four.

Size. Adults from 9.5 mm (male from type material) to 12.9 mm (♀ from type material) (Bruce, 1986). Specimens examined here from AM P47643 to c. 16 mm.

Remarks. *Natatolana bulba* is extremely similar to *N. kahiba*, comparison of their type specimens revealed only two characters to differentiate them: the number of robust setae on the uropod exopod lateral margin (none in *N. bulba*; two or three in *N. kahiba*); and the relative lengths of the antennae (in *N. bulba* reaching to the posterior of pereonite 3, 0.3–0.35× as long as the body with c. 18 flagellar articles; in *N. kahiba* reaching between pereonite 1 and 2, 0.2–0.25× as long as the body, with 12–15 flagella articles). Specimens without robust setae on the uropod exopod lateral margin but with short antennae corresponding to those found in *N. kahiba* were identified as *N. bulba* as noted in "variation". Allozyme analysis comparing specimens with this morphology, with that of *N. kahiba*, shows that recognition of separate species is warranted (Keable, 1996b).

The most distinctive feature of *Natatolana bulba* is the lack of robust setae on the lateral margin of the uropod exopod. Similar species recorded here, which may also lack these setae, include *N. arrama*, *N. nammuldi* and *N. wowine*. These species can be most readily separated from *N. bulba* by the shapes of the frontal lamina, appendix masculina, posterolateral margins of pleonite 4, and the uropods and the number of robust setae on the pleotelson.

Using the key provided by Bruce (1986) *Natatolana bulba* can only be reached if it is assumed in couplet 21 that it has six or more robust setae on the pleotelson, whereas the type specimens only have four.

Distribution and ecology. Australia: Queensland, New South Wales, and Tasmania. At depths of 5–1000 m. Scavenger.

Natatolana buzwilsoni n.sp.

Figs. 9–10

Type material. HOLOTYPE: ♂, 14 mm, AM P47241. PARATYPES: All North-West Shelf, WA, collected CSIRO; ♀, AM P47242, 19°29.9'S 118°52.0'E, 37 m, 24 Oct. 1983, 05-D1-S; ♂, AM P47243, 19°04.4'S 118°47.5'E, 82–83 m, 16 Feb. 1983, 01-B6-S; ♂, AM P47244, 19°29.9'S 118°52'E, 38 m, 25 Oct. 1993, 05-D9-S. • Type locality: North-West Shelf, WA, Australia, 19°56.9'S 117°53.7'E, 42–43 m, [22 May 1983, 02-B2-S].

Diagnosis. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 2*: ventral posterolateral margin not produced. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.71× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins broadly rounded; apex not produced, lateral margins converging smoothly to a point; with 5 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.53× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal half. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1.01× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, acute. *Uropods*: exopod short, 0.78× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 3.2× width. Colour cream-white in alcohol. Chromatophores absent. *Eyes*: with 10 ommatidia in horizontal diameter; with 10 ommatidia in vertical diameter; round; without pigment in alcohol. *Frontal lamina*: length c. 3.2× basal width; apex expanded, anterior margin angled. *Antennule*: short, just reaching pereonite 1. Peduncular article 1 longer than article 2; article 2 with 1 large pappose

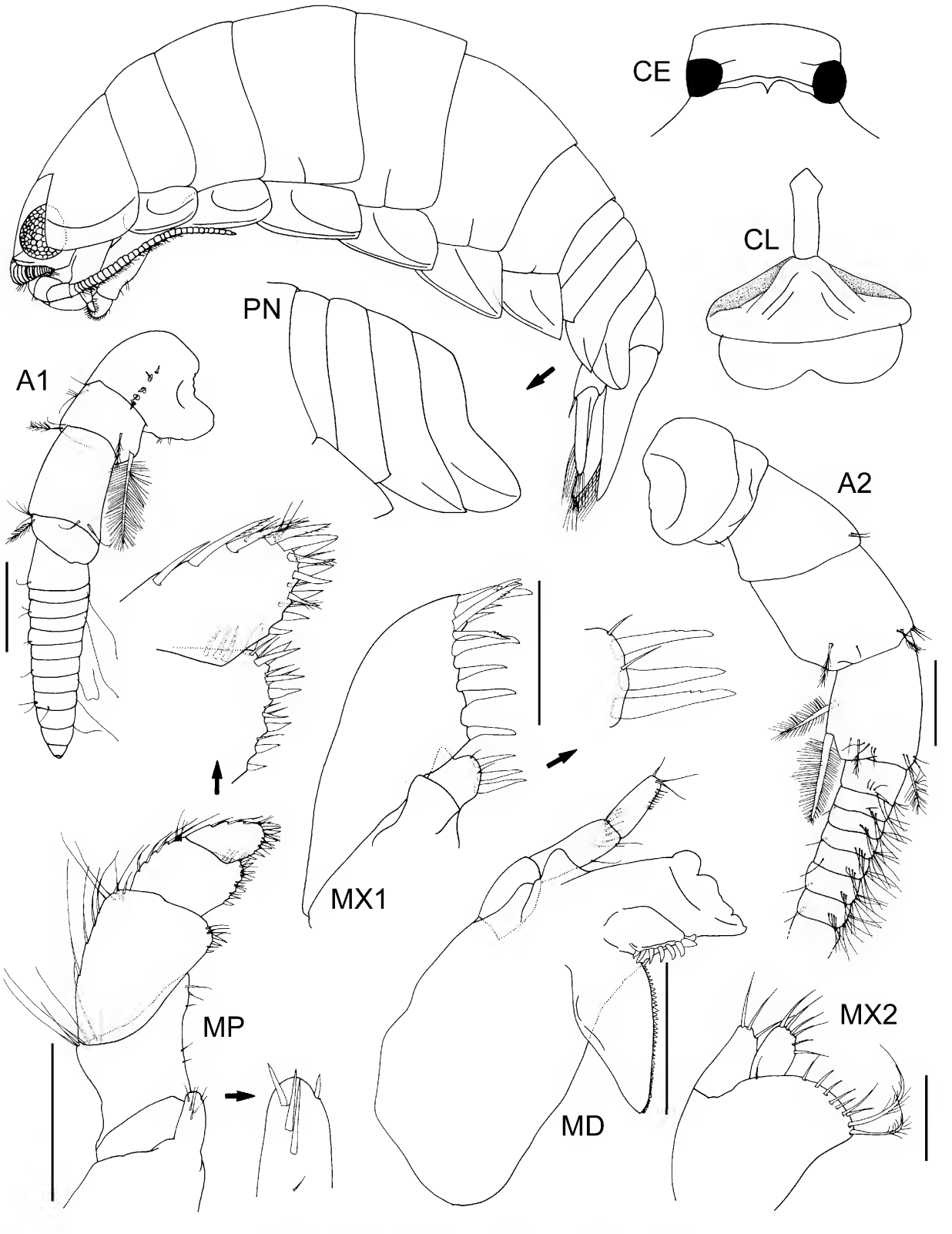

Fig. 9. *Natatolana buzwilsoni* n.sp., holotype. Scales = 0.5 mm.

seta; article 3 short, subequal to article 1. Flagellum 13-articulate. *Antenna*: peduncular article 4 with short penicillate and SS at distal margin; article 5 subequal in length to article 4, with 2 pappose setae on posterolateral margin, short penicillate and SS along distal margin. Flagellum 35-articulate. *Mandible*: incisor narrow, with posterior tooth not strongly developed; setal row with 8 RS. *Maxillule*: medial lobe with 3 large RS; lateral lobe with 11 RS on distal surface. *Maxilla*: lateral lobe broad, with 3 SS; medial lobe with 7 SS and 2 PS; middle lobe reduced, with 6 SS. *Maxilliped*: palp medial margin RS present. Endite with coupling hooks absent, 4 SS present. *Pereon*:

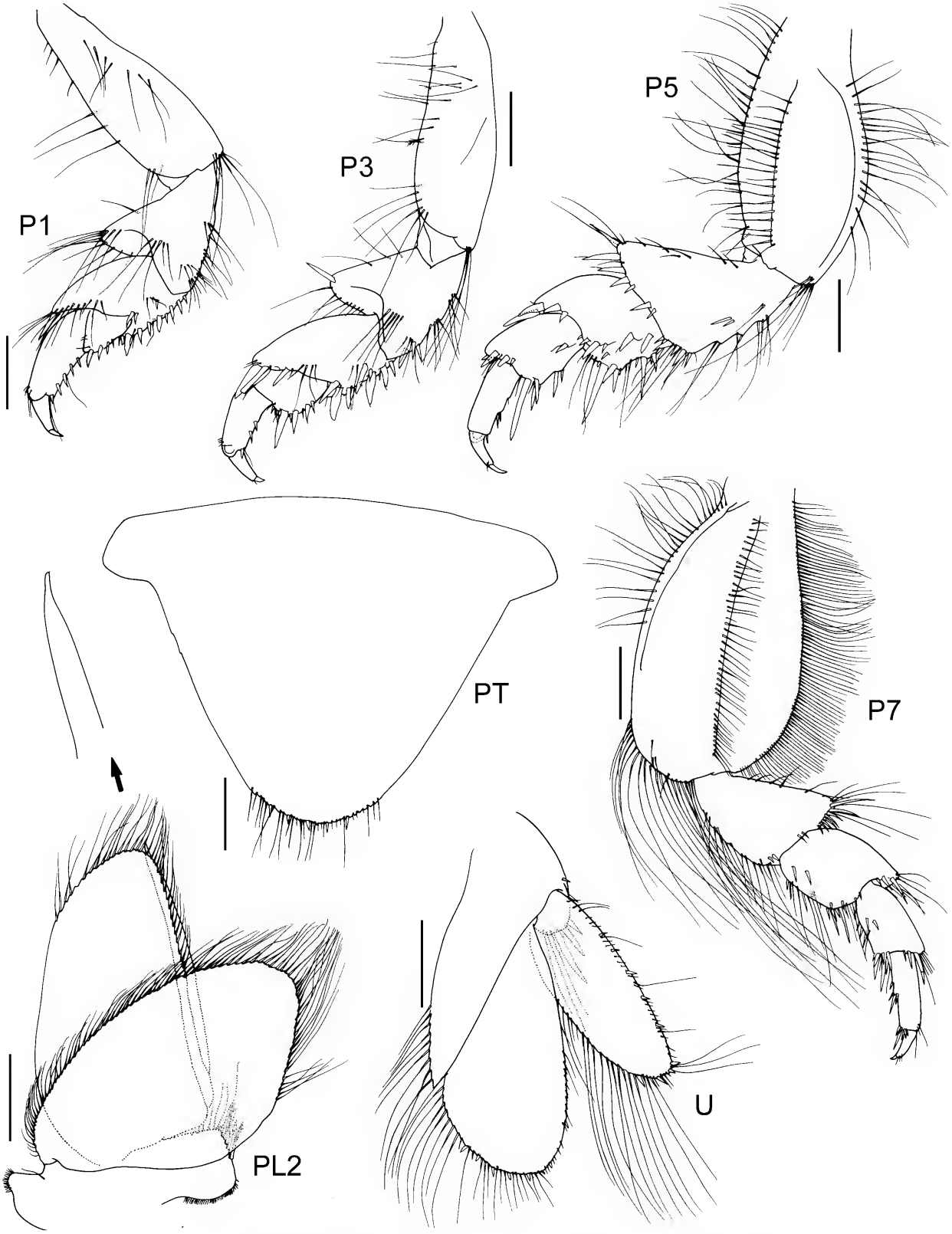

Fig. 10. *Natatolana buzwilsoni* n.sp., holotype. Scales = 0.5 mm, except MX2 = 0.2 mm.

ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with SS; posterior margin convex, PS present. Ischium width subequal to length; anterior margin with SS; posterior margin without RS, SS present. Merus posterior margin with 3 RS (and 2 submarginal RS), SS present. Carpus posterior

margin with 5 RS, 1 SS. Propodus subequal to carpus; posterior margin with 4 RS, SS. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod subcircular; medial margin rounded, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, curving in slightly before apex, with 1 RS, PS on distal half. Exopod ovate; medial margin convex, with 2 RS, PS on distal two-thirds; apex rounded, with 2 RS; lateral margin convex, with 5 RS, PS along entire length.

Variation. The holotype has five robust setae on the pleotelson as does one of the male paratypes. The other male paratype has six robust setae and the female paratype has four robust setae here.

Size. Adults to c. 14 mm.

Etymology. Named after Dr George (Buz) Wilson, in recognition of the help he has given me with this study.

Remarks. The mouthparts of *Natatolana buzwilsoni* are unusual; the narrow incisor of the mandible and lack of coupling hooks on the maxilliped endite occur in *N. endota, N. prolixa* and *N. karkarook*. *Natatolana helenae* also has a narrow mandible incisor. A reduction of the lateral lobe and middle lobe of the maxilla is also found in *N. karkarook*. The lack of setules on the robust setae of the maxillule medial lobe is a unique character state within the genus. The robust setae on the medial margin of the maxilliped palp are also unlike those found in other species.

Natatolana buzwilsoni is superficially similar to *N. pilula* but differs in numerous characters, most noticeably in having a broadly rounded pleotelson with robust setae, rather than a truncate pleotelson lacking robust setae. The apex of the appendix masculina is also distinct in the two species, being tapered to an acute point in *N. buzwilsoni*, whereas in *N. pilula* it forms a minute digitiform process.

Distribution. Australia: known only from the North-West Shelf of Western Australia. At depths of 37–83 m.

Natatolana caeca (Dollfus, 1903)

Synonymy in Keable & Bruce, 1997: 671, figs. 5–7.

Type material. Syntypes: all IOM; 138 specimens, 36 0188, Station 318; 2 specimens, 36 0189, Station 506; 5 specimens, 36 0184, Station 769; 5 specimens, 36 0185, Station 1048; 2 specimens, 36 0186, Station 1.100. All examined. • Type locality: all Méditerranée, (*Campagnes de l'Hirondelle et de la Princesse Alice*, 38°37'N 13°5'E, 1210 m, [Station 318]; 43°36'N 5°17'E, 1503 m, [Station 506]; 43°28'N 5°25'E, 2368 m, [Station 769]; 41°47'N 4°54'E, 2276 m, [Station 1048]; 43°02'N 6°22'E, 2500 m, [Station 1.100]).

Material examined. Listed by Keable & Bruce (1997).

Diagnosis. *Eyes*: absent. *Interocular furrow*: well developed, forming a ridge that extends across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.25× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows completely absent on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.98× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 8 RS. *Pereopods 1–6*: males with RS on the merus of pereopods 1–3, and carpus of pereopods 4–6, shorter than the propodus. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: ischium anterodistal angle produced, but not as produced as on pereopods 1 and 2, similar to pereopod 4. Propodus with 2 RS on palm. *Pereopod 7*: basis narrow, width 0.46× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.07× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.81× the length of the endopod.

Size. Adults to 15 mm.

Remarks. Keable & Bruce (1997) redescribe *Natatolana caeca* and discuss its identification and character variation. The reduced anterodistal angle of the ischium of pereopod 3 and absence of eyes are particularly useful characters for identifying this species.

Distribution. Material recorded by Keable & Bruce (1997) and the records of Hansen (1890) and Monod (1930) are from the northeast Atlantic between c. 18° to 50°N and 6° to 17°W. Only the type material has been recorded from the Mediterranean Sea. Most records are from the vicinity of about 1000 m depth, but the type specimens come from a maximum depth of 2500 m and a reliable minimum depth of 486 m is recorded by Keable & Bruce (1997).

Natatolana californiensis (Schultz, 1966)

Cirolana californiensis Schultz, 1966: 14, pl. 8.–1969: 178, fig. 276.–Brusca & Ninos, 1978: 379, figs. 1–7.

Cirolana deminuta Menzies & George, 1972: 19, figs. 12–13.–Brusca & Ninos, 1978: 379.–Bruce, 1986: 218.

Natatolana californiensis.–Bruce, 1981: 958.–1986: 218, 222.–Brusca & Iverson, 1985: 37, fig. 11E.–Brusca *et al.*, 1995: 84, figs. 65A, 66, 67.–Espinosa-Pérez & Hendrickx, 2001: 48.

Type material of *N. californiensis*. Holotype: male (not female as originally recorded), 8.0 mm, LACM 60.88.4, AHF Type No. 6048 (Brusca *et al.*, 1995). Paratypes: 2 (apparently 1 lost as Schultz (1966) indicated 3 specimens in addition to the holotype), LACM 60.76.3, AHF Cat. No. 952-1 San Clemente Island, Tanner Canyon, 54.8 km. 250°T from China Point Light, Channel Islands, Los Angeles County, California, USA, 32°37.87'N 118° 58.70'W, 792 m, RV Velero IV, Sta. 6833-60, 29 Jan. 1960 (Wetzer *et al.*, 1991; Brusca *et al.*, 1995). None examined. • Type locality of *N. californiensis*: Coronado Canyon, southern California, USA. Originally cited as 32°37'54"N 118°55'40"W, 812 m, [Velero IV station 6851] but emended to 32°30.70'N 117°21.62'W, 8.6 km, 322.5°T from North Coronado Island, San Diego County, on green mud, 794 m, [Velero IV Sta. 6851-60, 1 Feb. 1960] (Wetzer *et al.*; Brusca *et al.*, 1995).

Type material of *N. deminuta*. Holotype: ♀, 17 mm, USNM 121749 (examined). • Type locality of *N. deminuta*: Peru-Chile Trench, 7°58'S 80°37'W, 1005–1124 m, [Anton Bruun Station 88].

Material examined. **USA**: 33, USNM 113588, SW of San Clemente Island, California, 32°41.6'N 118°41'W, Hagfish trap, Hubbs, Newman *et al.*, 26–27 Sep. 1965, Agassiz stn MV 65.III.35.

Diagnosis. *Eyes*: absent or vestigial (there can be a small patch indicating vestigial ommatidia). *Interocular furrow*:

moderately developed, distinct but not extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.45× as long as body, reaching to approximately half way along pereonite 4. *Coxal plates*: furrows moderately developed on coxae 2–4 and strongly developed on coxae 5–7. *Pleonite 4*: apex forming a broad acute point or rounded (mostly produced into a broad acute point but in a few specimens it is worn into a rounded shape). *Pleotelson*: broad, length 0.77–0.88× basal width; anterodorsal depression absent (but with shallow paired submedian depressions near base that do not form a distinct and abrupt depression as in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 6–10 RS. *Pereopod 2*: propodus with 1–3 RS on palm. *Pereopod 3*: propodus with 1–3 RS on palm. *Pereopods 5–7*: propodus long, on pereopod 5 greatly elongate, 2× that of pereopod 7. *Pereopod 7*: basis narrow, width 0.35–0.47× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length (Brusca *et al.* (1995) do not show setae on this margin. Their illustration, however, is a lateral view (no medial carina shown). In the material examined here, the short slender setae occurring along the length of this margin are difficult to see and would not be apparent in a lateral view). *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.09× length of endopod; margins very strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.86× the length of the endopod.

Variation. Brusca & Ninos (1978) recorded a range of 10–21 articles for the antennal flagellum, Brusca *et al.* (1995) give a range of 10–22. In the smallest subadult examined here there is at least 17 articles. Possibly the figure of 10 articles was based on the illustration of *C. deminuta* by Menzies & George (1972), which is erroneous.

Size. Adults to 13.4 mm.

Remarks. Schultz (1966) did not illustrate an interocular furrow for *Natatolana californiensis*. In the material examined, however, a distinct, incomplete interocular furrow is apparent. Brusca & Ninos (1978) synonymized *N. deminuta* with *N. californiensis*. The holotype of *N. deminuta* has the apex of the pleotelson more produced than that described for *N. californiensis* and appears to have had 12–14 robust setae on the pleotelson, many of which have been broken off. Brusca & Ninos (1978) recorded the range of robust setae on the pleotelson of *N. californiensis* as six to 12 but this was modified by Brusca *et al.* (1995) as six to 10. The illustration of Brusca *et al.* (1995) shows eight robust setae on the pleotelson margins of the holotype of *N. californiensis*. Of the material examined here, the most common number of robust setae on the pleotelson is eight although some specimens have nine. The material of *N. californiensis* examined here and the holotype of *N. deminuta* both have a broad acute posterolateral margin on pleonite 4. It is, however, somewhat narrower and less rounded in the holotype of *N. deminuta*. The holotype of *N. californiensis* lacks setae on the endopod of pleopod 5 (Brusca *et al.*, 1995), but these are present on the holotype of *N. deminuta* (pers. obsv.). Given these differences, and the distance between the type locality of *N. deminuta* and records of *N. californiensis*, they may not be synonyms. The holotype of *N. deminuta*, however, is in poor condition and, because it is a female, diagnostic characters, such as the shape of the appendix masculina or presence of penes, cannot be assessed. Therefore, further material from the proximity of the type locality of *N. deminuta* is needed to resolve the question of whether it represents a valid species of *Natatolana* or a synonym of *N. californiensis*.

Distribution and ecology. *Natatolana californiensis* has been recorded from the west coast of North, Central and South America. The species has mostly been recorded from southern California and Mexico, with a single record from Costa-Rica (Brusca *et al.*, 1995; Espinosa-Pérez & Hendrickx, 2001). The holotype of *Natatolana deminuta* that Brusca & Ninos (1978) synonymized with *N. californiensis* was collected from the Peru-Chile Trench. Brusca & Ninos (1978) indicated that most specimens are collected at depths of 700–2000 m, although a few specimens have been collected from depths as shallow as 40 m and 250 m. Alternatively, Brusca *et al.* (1995) cite the distribution as including depths of 792–1250 m. Scavenger (some of the material examined in this study was from a hag fish trap and was therefore presumably scavenging on bait or the catch in the trap).

Natatolana carlenae Brusca, Wetzer & France, 1995

Natatolana carlenae Brusca *et al.*, 1995: 84, figs. 65B, 68–70.–Espinosa-Pérez & Hendrickx, 2001: 48.

Natatolana carlanae.–Espinosa-Pérez, & Hendrickx, 1997: 39 [*lapsus*].

Type material. Holotype: ♂, USNM 252731 (not examined). Paratypes: 5♂♂ and ♀♀ from type locality, USNM 252732 (not examined); numerous additional paratypes from Mexico, Baja California and several from Costa Rica and Panama in USNM and LACM of which 2♀♀, manca, USNM 252742, Los Angeles Bay, Baja California, Mexico, Gulf of California, 59 m, Velero III Station 701-37 examined. • Type locality: Tiburon Island, Sonora, Gulf of California, Mexico, [c. 29°N 112°30'W], on muddy sand, 73–101 m, [Sta. No. 563-36, USNM acc. no. 139772, 10 Mar. 1936].

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.35–0.4× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed, weakly developed and incomplete on anterior coxae, absent on coxa 6 and incomplete on coxa 7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.82× basal width; anterodorsal depression absent (with a pair of shallow submedian depressions near base that do not form a distinct and abrupt depression as in species such as *N. pellucida*); anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 10–14 RS (holotype illustrated as having 12, material examined with 12). *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis broad, width 0.55× length; distance between anterior margin and medial carina less than between posterior margin and

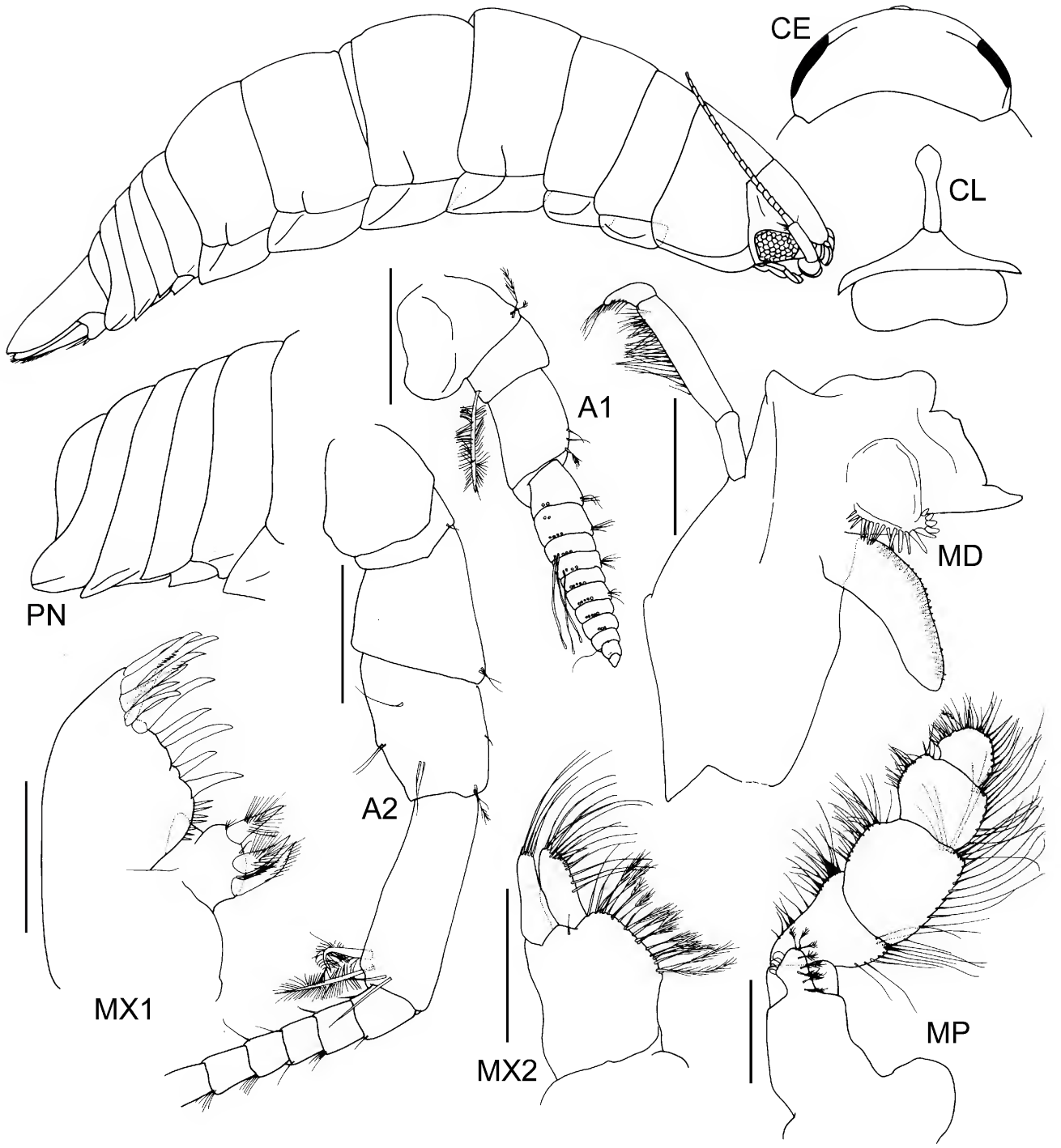

Fig. 11. *Natatolana chilensis*, male paratype SMNH 3182. All scales = 0.5 mm.

medial carina; posterior margin with setae proximally and distally but not medially. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.94× the length of the endopod.

Size. Adults to 16.8 mm.

Remarks. *Natatolana carlenae* is very similar to *N. nukumbutho* but differs in having coxal furrows only on the anterior coxae, pereopod 7 with a slightly broader basis and pleonite 4 with slightly broader posterolateral margins.

Distribution. North/Central America: northwest Baja California (Pacific), the Gulf of California, Costa Rica, and Panama. At depths of 9-1168 m but mostly recorded from depths of 9–165 m, rarely from 247–1168 m.

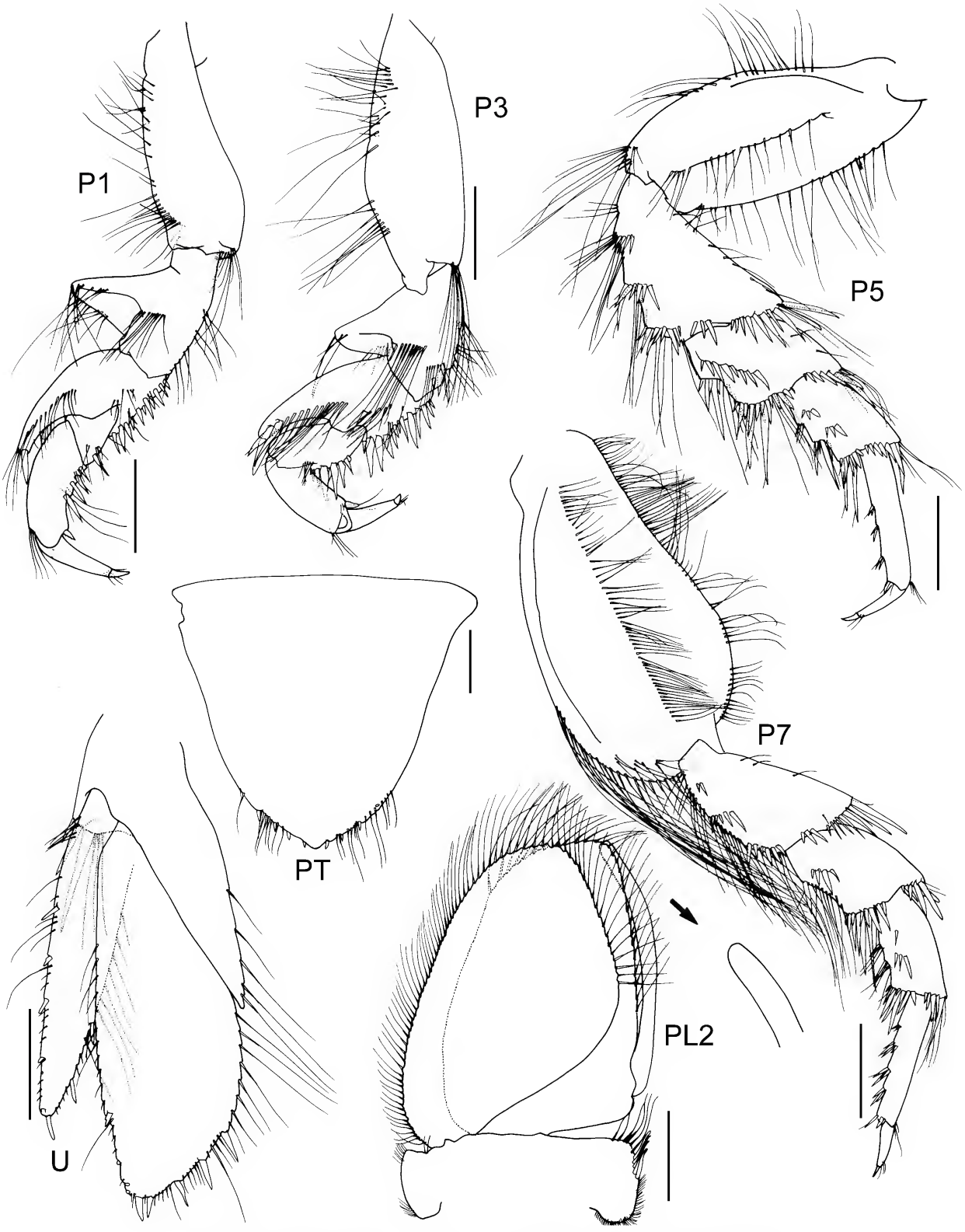

Fig. 12. *Natatolana chilensis*, male paratype SMNH 3182. All scales = 0.5 mm.

Natatolana chilensis (Menzies, 1962)

Figs. 11–12

Cirolana chilensis Menzies, 1962: 122, fig. 39 A–E.–Carvacho, 1977: 40.–Ríos *et al.*, 2003: 6.

Natatolana chilensis.–Bruce, 1981: 958.–1986: 222.–Brusca *et al.*, 1995: 80.

Type material. Holotype: ♂, 19.6 mm, SMNH 3181; allotype, ♀, 22.4 mm, SMNH 3181. Paratypes: 46 specimens, SMNH 3182. All examined. • Type locality: the bay east of the church on Isla Quellín, Seno Reloncaví, Southern Chile, 41°52'30"S 72°53'50"W, 25 m, [Lund University Chile Expedition 1948–49, Station M 39].

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.34× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.87× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins convex; apex produced into a small point; with 8–10 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis broad, width 0.54× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent (area around openings slightly raised but not forming flexible processes). *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.97× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.82× the length of the endopod.

Additional descriptive characters. Based on paratype, male, 20 mm. *Body*: length c. 3.41× width. Colour cream in alcohol. Chromatophores present, or absent (there appear to be minute traces of chromatophores); small; red/brown/grey in alcohol; scattered over body. *Eyes*: with 8 ommatidia in horizontal diameter; with 7 ommatidia in vertical diameter; ovate; colour red/brown in alcohol. *Frontal lamina*: length c. 4.8× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 short, subequal to article 1. Flagellum 11-articulate. *Antenna*: peduncular article 4 with several SS posteromedially, 1 PS and 1 penicillate seta at anterodistal angle; article 5 with 2 PS and 2 pappose setae at posterodistal angle. Flagellum 26-articulate. *Mandible*: setal row with 18 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 5 SS; medial lobe with 7 SS and 14 PS; middle lobe with 15 SS. *Maxilliped*: endite with 3 coupling hooks, and 8 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–7; pereonites 1 and 5–6 subequal in length and longest, 4 and 7 subequal and longer than 2–3 which are subequal. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin sinuate; medial carina with PS and SS present (plumose setae sparse, a few proximally and distally, slender setae along entire length); posterior margin convex. Ischium anterior margin with SS (sparse); posterior margin with 7 RS, PS and SS present. Merus posterior margin with 5 RS, SS present. Carpus posterior margin with 4 RS (and 4 submarginally), SS present. Propodus longer than carpus; posterior margin with 12 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture feebly developed (complete but very faint) on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 3 RS, PS on distal two-thirds. Exopod medial margin convex, with 2 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 4–6 RS, PS on distal three-quarters.

Variation. Ten paratype specimens were examined for variation in the number of robust setae occurring on the margins of the pleotelson. Of these 20% have 10, 10% have nine and 70% have eight.

Size. Adults to c. 22.4 mm.

Remarks. The dorsal view illustration of *Natatolana chilensis* by Menzies (1962) is misleading showing far more articles than are present in the antennal flagellum.

This species is similar to a number of others, including *Natatolana woodjonesi* as noted by Menzies (1962). The incomplete interocular furrow, complete coxal furrows on all coxae, absence of penes, sinuate posterodorsal margin of pleonite 4, convex posterolateral margins of the pleotelson converging smoothly to a point with eight to 10 robust setae, and presence of robust setae on the propodal palm of pereopods 2 and 3, are, however, sufficient characters to distinguish *N. chilensis* from all other species in the genus.

Distribution. Chile: several localities. In depths of 12–60 m.

Natatolana corpulenta (Hale, 1925)

Fig. 13

Cirolana corpulenta Hale, 1925: 134, fig. 3 (part).–1929: 248, fig. 239.–Nierstrasz, 1931: 157.–Poore *et al.*, 1975: 33.

Natatolana corpulenta.–Bruce, 1981: 958.–1986: 79, figs. 51, 53 (part).–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Not *Cirolana corpulenta*.–Hale, 1940: 289 [mis-identification = *Natatolana longispina* Bruce, 1986; *Natatolana sinuosa* n.sp.].

Type material. Holotype: ♀, SAMA, C275. Paratypes: 35 specimens, SAMA C276; ♀, SAMA C277. All examined. • Type locality: Port Willunga, South Australia, Australia, [35°16'S 138°28'E].

Material examined. **New South Wales**: manca, AM P23040, 500 m east of Merewether Beach, 32°57'S 151°45'E, Shipek [grab] collection transect, 15 m, AM Hunter District Water Board Survey, 30 Nov. 1975 (reported by Bruce [1986]); series from off Grotto Point, Port Jackson, baited trap; 434, AM P47464, 33°49.05'S 151°15.8'E, on sediment, 15 m, S. Keable & J. Lowry, 8–9 May 1988, site 13; 418, AM P38674, 33°49.2'S 151°15.75'E, unknown substrate, probably sediment, 10 m, S. Keable, J. Lowry & D. Townsend, 16–17 Jul. 1988, Site 37; 1, AM P47645, 33°49.2'S 151°15.55'E, baited trap on sediment a few metres from rocky shore, 3 m, S. Keable, J. Lowry & D. Townsend, 16–17 Jul. 1988, site 38. **Tasmania**: series from off St Helens Point, c. 41°17.3'S 148°21'E (except as noted), baited trap, J. Lowry, S. Keable & C. McCormick, 13–16 April 1991; 64, AM P47456, sandy bottom, 15 m, TAS-124; 70, AM P47457, sandy bottom, 5 m, TAS-125; 229, AM P47458, sandy bottom, 10 m, TAS-126; 13 mancas, AM P47459, off rocks at northern end, sandy bottom, 15 m, TAS-139; 1, AM P47462, inside breakwater, Blanche Point, Georges Bay, 41°17.05'S 148°19.9'E, sand bottom, 12 m, TAS-161; 50, AM P47460, in the cove off Beerbarrel Beach, 41°17.2'S 148°21.3'E, sandy bottom, 10 m, TAS-127; 1, AM P47461, off Binalong Beach, Binalong Bay, 41°14.7'S 148°17.6'E, on sand, 8 m, TAS-144; 2, AM P47463, about 25 m off middle of breakwater, Pilot Bay, 42°12.4'S 145°12.4'E, baited trap, unknown substrate, probably sand, 6 m, J. Lowry & S. Keable, 26–27 April 1991, TAS-286.

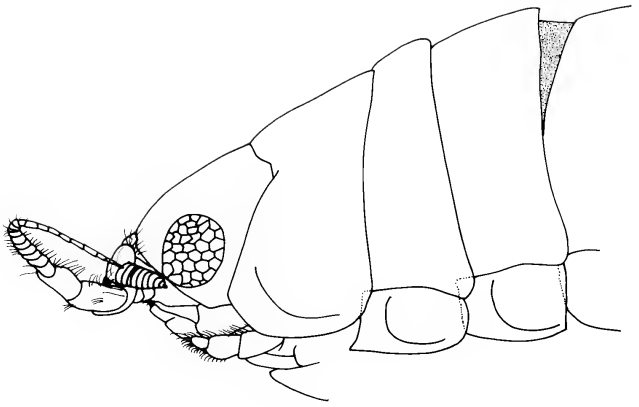

Fig. 13. *Natatolana corpulenta*, female, 19 mm, AM P47458.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.27× as long as body, reaching to just beyond the posterior margin of pereonite 2. *Coxal plates*: furrows strongly developed, on all coxae. Coxa 2 with anteroventral corner produced into an acute tooth. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a broad acute point. *Pleotelson*: broad, length 0.7× basal width; anterodorsal depression present; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins concave; apex produced into a large point; with 10–12 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.47× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on distal half or along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.14× length of endopod; slender; margins very slightly curved laterally; apex recurved, bent slightly medially, bluntly rounded or acute. *Uropods*: exopod subequal to endopod, 0.99× the length of the endopod.

Variation. The female specimen described by Bruce (1986) from Point Leo, Victoria has only 10 robust setae on the pleotelson, not 12 as in the holotype. The male, 7.2 mm, from Stockton Beach, New South Wales, illustrated by Bruce (1986) has an acute apex on the appendix masculina whereas in a male, 15 mm, examined here from Tasmania (AM P47458) the apex was bluntly rounded. The material from New South Wales examined by Bruce (1986) has been re-examined (see remarks), most of it is not *Natatolana corpulenta*. Unfortunately it cannot be determined if the male illustrated by Bruce (1986) is among these specimens.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Adults to c. 12 mm.

Remarks. *Natatolana corpulenta* can be most easily separated from similar species by the presence of an acute produced tooth on the anteroventral corner of coxa 2. This tooth was illustrated and described in the holotype female of *N. corpulenta* but not emphasized (Hale, 1925) and was omitted in the redescription of the species by Bruce (1986). *Natatolana nitida* is the only other species of *Natatolana*, examined in this study, which has a similar tooth, although it is indicated in the illustrations of *N. pallidocula* and *N. anophthalma*.

Natatolana corpulenta has been confused with a number of other species. Hale (1940) stated that prior to his record, of a female specimen of *N. corpulenta* from Tasmania, only one other specimen (the type female) had been recorded. This is erroneous as Hale (1925) mentioned a single specimen from the body cavity of a Port Jackson shark collected at Brighton. Hale (1925) also stated that a small series of mostly immature specimens was obtained at Port Willunga. These additional specimens are registered in the collections of the South Australian Museum (C277 and C276 respectively) as paratypes of *N. corpulenta*. The specimen from the Port Jackson shark is a female of *N. debrae* n.sp. Of the 35 specimens from Port Willunga (SAMA C276), 29 are *N. corpulenta* and six are *N. sinuosa* n.sp. The female specimen recorded by Hale (1940) from Elliott Cove (as Eliott Cove), West Coast, Tasmania is held at the Australian Museum (E6757). This specimen is *N. longispina* not *N. corpulenta*. Hale (1940) also mentioned specimens sent to him from New South Wales by T.C. Roughley. These specimens are *N. sinuosa* not *N. corpulenta*. Three species are present in the material recorded by Bruce (1986) from the Australian Museum Hunter District Water Board Survey series, collected near Newcastle, NSW (P23034–40, P23042, P23047). The specimens from off Stockton Beach are *N. sinuosa*, those from off Belmont Beach are a mixture of *N. longispina* and *N. sinuosa*, and the specimen off Dudley Beach is *N. sinuosa*. Only the manca specimen from off Merewether Beach is *N. corpulenta*.

Apart from the tooth on coxa 2, *Natatolana corpulenta* can be separated from most other species of *Natatolana* by the shape and setation of the pleotelson which is similar to that illustrated by Bruce (1986). The concave posterolateral margins, with c. 12 robust setae and strongly produced acute apex are distinctive.

Natatolana pallidocula, known only from the holotype (not examined), appears to be extremely similar to *N. corpulenta*. Many important characters, such as the presence or absence of penes in males, have not been recorded for *N. pallidocula*. The description given by Kussakin & Vasina (1982a) indicates that *N. pallidocula* differs from *N. corpulenta* in having rectangular eyes with 14 ommatidia in the horizontal row (not oval with five ommatidia in the horizontal row), lacking conspicuously elongated robust setae on pereopods 1–6 in males and in having the appendix masculina of the male pleopod 2 slightly shorter than the endopod. The male characters, however, are only fully developed in mature specimens and the holotype of *N. pallidocula* could be immature.

Distribution and ecology. Australia: central New South Wales, Victoria, Tasmania, and South Australia. At depths of 3–15 m. Scavenger.

Natatolana curta (Richardson, 1910)

Cirolana curta Richardson, 1910: 7, fig. 6.–Nierstrasz, 1931: 156.
Natatolana curta.–Bruce, 1981: 958.–1986: 53, 74, 222.–Brusca *et al.*, 1995: 80.

Type material. Holotype: ♂, 18 mm, USNM 41013 (examined). • Type locality: between Jolo and Tawi Tawi, Dammi Island, [Philippines, 5°48'N 120°36'E], 441 m, [*Albatross* Station 5565].

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing posteriorly. *Antenna*: c. 0.39× as long as body, reaching to between the posterior of pereonite 3 and one-quarter of the way along pereonite 4. *Coxal plates*: furrows strongly developed, clearer on anterior coxae than posterior but all complete, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.71× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins broadly rounded; apex not produced, lateral margins converging smoothly to a point; with 11 RS. *Pereopod 2*: propodus with 4 RS on palm. *Pereopod 3*: propodus with 3 RS on palm. *Pereopod 7*: basis broad, width 0.6× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.92× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.68× the length of the endopod.

Sexual dimorphism. Unknown, but the male holotype has indistinct tubercules on the dorsal surface of pereonites 1 and 3 that may be absent in females.

Size. Adults to 18 mm.

Remarks. A description of the penes and appendix masculina of *Natatolana curta* have not previously been given. *Natatolana curta* is most similar to *N. albicaudata* and *N. amplocula*, see remarks for these species.

Distribution. Philippines. At depths of 441 m.

Natatolana debrae n.sp.

Figs. 14–16

Cirolana corpulenta.–Hale, 1925: 134 fig. 3 (part) [misidentification, not *Natatolana corpulenta* (Hale, 1925)].

Type material. HOLOTYPE: ♂, 9 mm, AM P31604. PARATYPES: ♀, 16 mm, ♀, 6.5 mm, manca, 6 mm, AM P47245. • Type locality: Henley Beach, Adelaide, South Australia, Australia, 38°56'S 138°31'E, low tide sand bar 20 m off shore, fine sand and shell, [J.K. Lowry, 29 Dec. 1976].

Additional material. South Australia, paratype female of *Natatolana corpulenta*, SAMA C277, Brighton [presumably Gulf St Vincent, 35°01'S 138°31'E], from body cavity of *Heterodontus phillipi*, H. Collyer.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.46× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows moderately developed, on all coxae. Pereonite 1, coxa 2 posterior margins sinuate, posteroventral corners developed into weak coxal points. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a broad acute point. *Pleotelson*: broad, length 0.9× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins concave; apex produced into a large point; with 10 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.42× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.05× length of endopod; margins sinuate; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.93× the length of the endopod; lateral margin with RS.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.11× width. Colour cream-yellow in alcohol. Chromatophores absent. *Eyes*: with 5 ommatidia in horizontal diameter; with 8 ommatidia in vertical diameter; ovate; colour brown in alcohol. *Frontal lamina*: length c. 3.8× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 short, subequal to article 1. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 5 SS medially on posterolateral margin, 4 SS on distal margin, 3 SS and 1 penicillate seta at anterodistal angle; article 5 with 2 conspicuous pappose setae and 1 SS at posterodistal angle, 3 SS on distal margin and 2 SS at anterodistal angle. Flagellum 20-articulate. *Mandible*: setal row with 16 RS. *Maxillule*: medial lobe with 3 large robust pappose setae and 2 SS; lateral lobe with 12 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 6 SS and 9 PS; middle lobe with 11 SS. *Maxilliped*: endite with 2 coupling hooks, and 7 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1; pereonite 1 longest, 4–6 subequal and longer than 2–3 and 7 which are subequal. *Coxae*: coxal points weakly developed on posteroventral corners of pereonite 1 and all coxae. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex, SS present. Ischium anterior margin with SS; posterior margin with 1 RS (and 2 submarginally), PS present. Merus anterior margin with SS; posterior margin with 1 RS (submarginal), SS present. Carpus anterior margin with 1 SS; posterior margin with 3 RS (and 1 submarginally), SS absent. Propodus subequal to carpus; posterior margin with 3 RS, SS absent. *Penes*: forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod triangular; medial margin slightly convex and obtusely angled proximal to peduncle, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 4 RS and 1 penicillate seta, PS along entire length. Exopod medial margin convex, with 3 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 8 RS, PS along entire length.

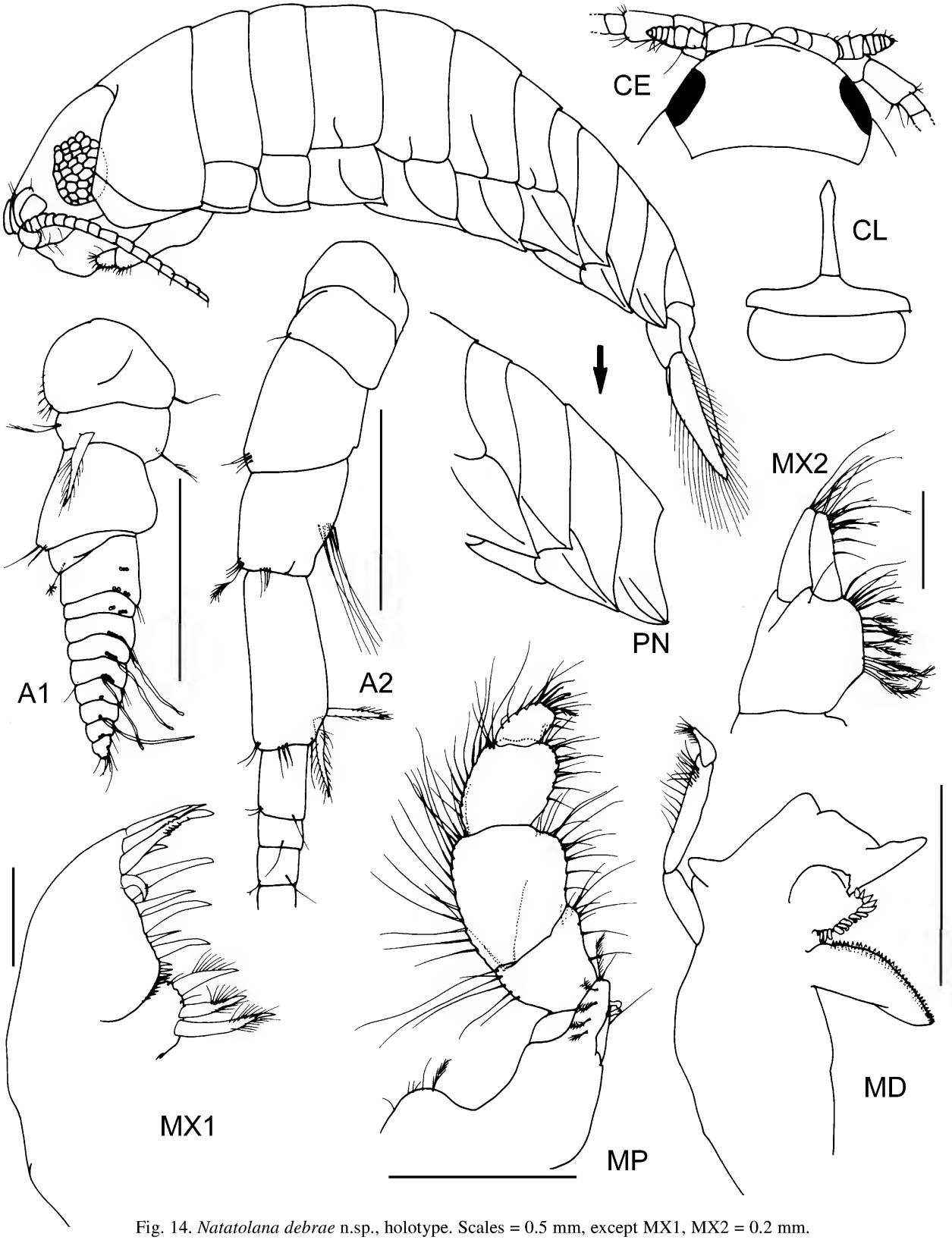

Fig. 14. *Natatolana debrae* n.sp., holotype. Scales = 0.5 mm, except MX1, MX2 = 0.2 mm.

Variation. The right uropod endopod of the holotype has two robust seta on the apex and four robust setae on the medial margin.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and the carpus of pereopods 4–6 of adult males.

Size. Adults to c. 16 mm.

Etymology. Named after my wife Debra, in recognition of the help she has given me during this and other projects.

Remarks. The specimen of *Natatolana corpulenta* recorded by Hale (1925) from the body cavity of a Port Jackson shark

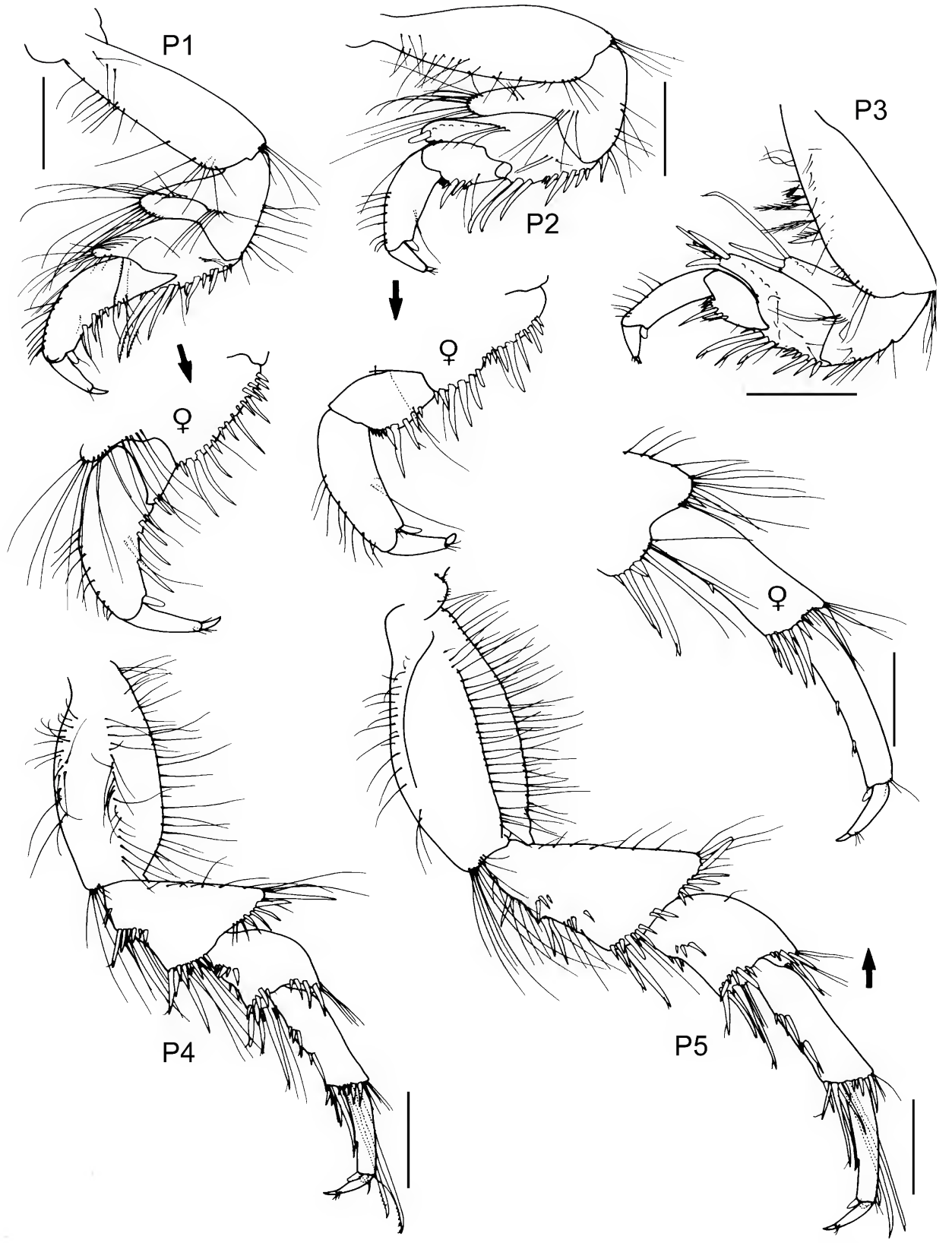

Fig. 15. *Natatolana debrae* n.sp., holotype, except; female = paratype female, AM P47245. Scales = 0.5 mm.

collected by H. Collyer at Brighton is registered in SAMA collections (C277) as a paratype of *N. corpulenta* but is actually a specimen of *N. debrae*.

Natatolana debrae is most similar to *N. corpulenta, N. femina* n.sp. and *N. sinuosa* n.sp. *Natatolana debrae* differs from *N. corpulenta* in lacking an acute produced tooth on the anteroventral corner of coxa 2; in having sinuate posterior margins developed into weak coxal points on the posteroventral corners of pereonite 1 and coxae 2–3; and in having longer antennae. *Natatolana sinuosa* and *N. femina*

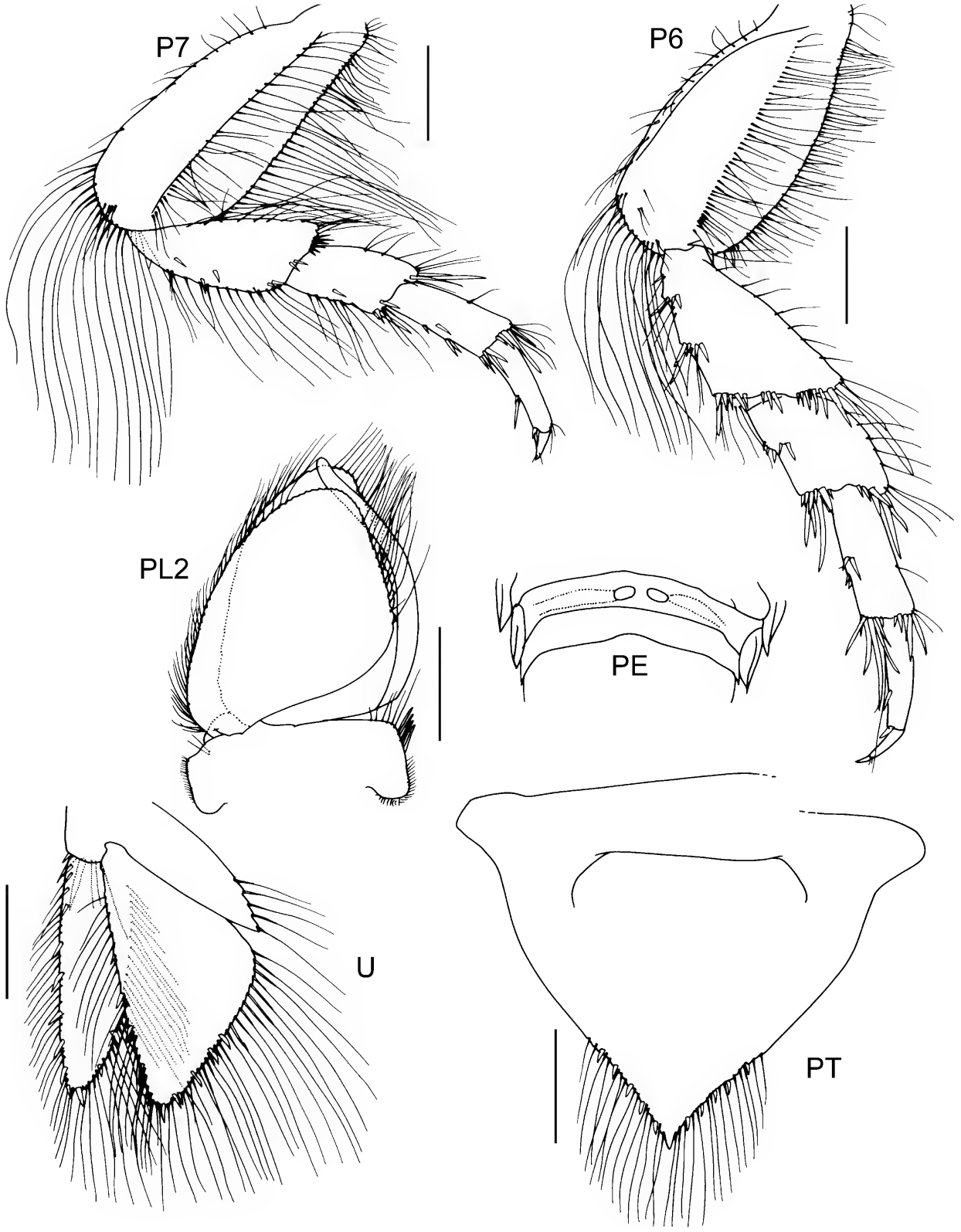

Fig. 16. *Natatolana debrae* n.sp., holotype. Scales = 0.5 mm, except MX1, MX2 = 0.2 mm.

can be readily distinguished from *N. debrae* by the development of coxal points on the posteroventral corners of pereonite 1 and coxa 2–3 (much stronger in *N. sinuosa* and rounded in *N. femina*).

Distribution and ecology. Australia: known only from Gulf St Vincent, South Australia. Apparently intertidal and subtidal. Scavenger (specimens have been recorded from the body cavity of a Port Jackson shark).

Natatolana endota Bruce, 1986

Natatolana endota Bruce, 1986: 63, figs. 38, 39.–Springthorpe & Lowry, 1994: 44.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♂, 12.8 mm, AM P32172 (examined). Paratypes: AM P10693, P10689 (examined); TM G1505 (not examined). • Type locality: off Sow and Pigs Shoal, Port Jackson, NSW, Australia, 33°20'S 151°16'E, 10 m.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 1.3× as long as body, reaching to beyond pleotelson. *Coxal plates*: furrows variously developed, indistinct furrows on coxae 2–4 only. *Pleonite 2*: ventral posterolateral margin acute, formed into long curved process. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.76× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, contiguous with anterolateral margins; apex narrowly rounded; with 4 RS. *Pereopods 1–6*: males with the RS on the merus of pereopods 1–3, and carpus of pereopods 4–6 shorter, than the propodus. Pereopod 2: propodus with 8 RS on palm. *Pereopod 3*: propodus with 8 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.52× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal half. *Penes*: present (although Bruce (1986) describes the vas deferens as opening flush to the surface of the sternite). *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; slender; margins very slightly curved laterally; apex not at angle to adjacent margins, acute. *Uropods*: exopod subequal to endopod, 1× the length of the endopod.

Size. Adults to 13.9 mm.

Remarks. The antennular flagellum of *Natatolana endota* was described by Bruce (1986) as being longer than the peduncle but the illustration provided and examination of specimens indicates that it is shorter. *Natatolana endota* is readily distinguished from other species in having antennae that reach beyond the pleotelson and a pleotelson with straight lateral margins that converge to a narrowly rounded apex that has four robust setae.

Distribution. Australia: Port Jackson, New South Wales; northern Tasmania At depths of 9–23 m.

Natatolana femina n.sp.

Figs. 17–19

Type material. HOLOTYPE: ♀, 12.5 mm, AM P47232. PARATYPES: ♂, 10 mm, AM P47233, same data as for holotype except off the rocks on the north end of Maurouard Beach, 41°17.3'S 148°21.3'E, 15 m, TAS-124; 7 specimens, TM, same data as holotype. • Type locality: in the corner off the northern end of Maurouard Beach, St Helens Point, Tasmania, Australia, 41°17.3'S 148°20.9'E, [baited trap], sandy bottom, 5 m, [J. Lowry, S. Keable & C. McCormick, 13–14 April 1991, TAS-125].

Additional material. **Tasmania**: 18 mancas, AM P47234, off rocks at the northern end of Maurouard Beach, 41°17.3'S 148°21'E, 10 m, TAS-126; 6 mancas, AM P47235, same data as holotype except in the cove off Beerbarrel Beach, 41°17.2'S 148°21.3'E, 10 m, TAS-127; 29 mancas, AM P47236, same data as holotype except off Binalong Beach, Binalong Bay, 41°14.7'S 148°17.6'E, 8 m, 14–15 April 1991, TAS-144.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows weakly developed, on all coxae. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a broad acute point. *Pleotelson*: broad, length 0.87× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins concave; apex produced into a large point; with 12–15 RS. *Pereopods 1–6*: males with the RS on the merus of pereopods 1–3, and carpus of pereopods 4–6, shorter than the propodus (but fully mature males not known). *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.57× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent, vasa deferentia opening flush to surface of sternite 7 (but fully mature males not known). *Pleopod 2 appendix masculina*: just shorter than endopod, 0.88× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded (but fully mature males not known). *Uropods*: exopod subequal to endopod, 0.98× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.7× width. Colour translucent white to yellow in alcohol. Chromatophores present; both large and small; grey in alcohol; restricted to lateral margins of pereonites, pleonites and coxae, fairly sparse and faint, fading after preservation. *Cephalon*: submarginal cephalic furrow absent. Eyes: with 5 ommatidia in horizontal diameter; with 9 ommatidia in vertical diameter; ovate; colour red-brown in alcohol. *Frontal lamina*: length c. 3.85× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 and article 2 subequal in length; article 2 with several small penicillate setae on lateral margins and 1 large pappose seta on medial anterolateral margin; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 14-articulate. *Antenna*: peduncular article 4 with numerous long SS on posterolateral margin, several short SS and 1 penicillate seta at anterodistal angle; article 5 with 2 pappose setae and 4 SS at posterodistal angle, 4 SS at anterodistal angle. Flagellum 27-articulate. *Mandible*: setal row with 19 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae and 2 small SS; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 3 SS and 17 PS; middle lobe with 17 long SS on outer row and 4 short SS on inner row. *Maxilliped*: endite with 2 coupling hooks, 5 PS and 2 SS. *Pereon*: ornamentation consists of 1 weakly developed furrow on lateral margin of pereonite 1; pereonites 1 and 5–6 subequal in length and longest, 4 and 7 subequal and longer than 2–3 which are subequal. *Coxae*: pereonite 1, coxae 2–4 with rounded posteroventral corners, coxae 5–6 with sinuate posterior margins developed into small coxal points, coxa 7 with a produced, broad, acute posteroventral corner. *Pleonite 2*: dorsal posterolateral margin subequal with ventral

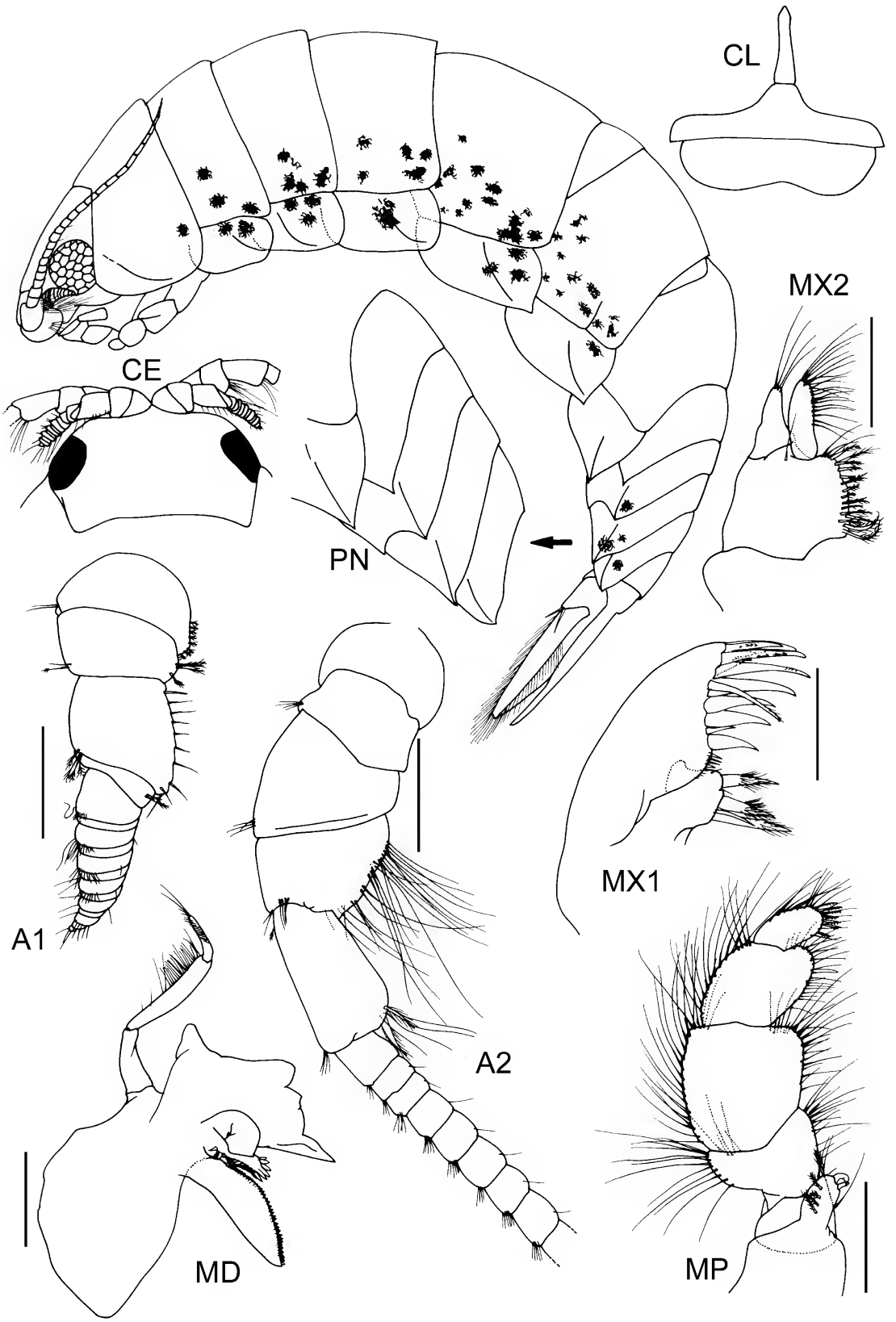

Fig. 17. *Natatolana femina* n.sp., holotype. Scales = 0.5 mm.

posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex, SS present. Ischium anterior margin with SS; posterior margin with groups of RS present, PS present. Merus anterior margin with SS; posterior margin with 5 RS (1 proximal and 1 group of 4 medially), SS present. Carpus anterior margin with SS; posterior margin with 6 RS, SS absent. Propodus subequal to carpus; posterior margin with 5 RS, SS absent. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most

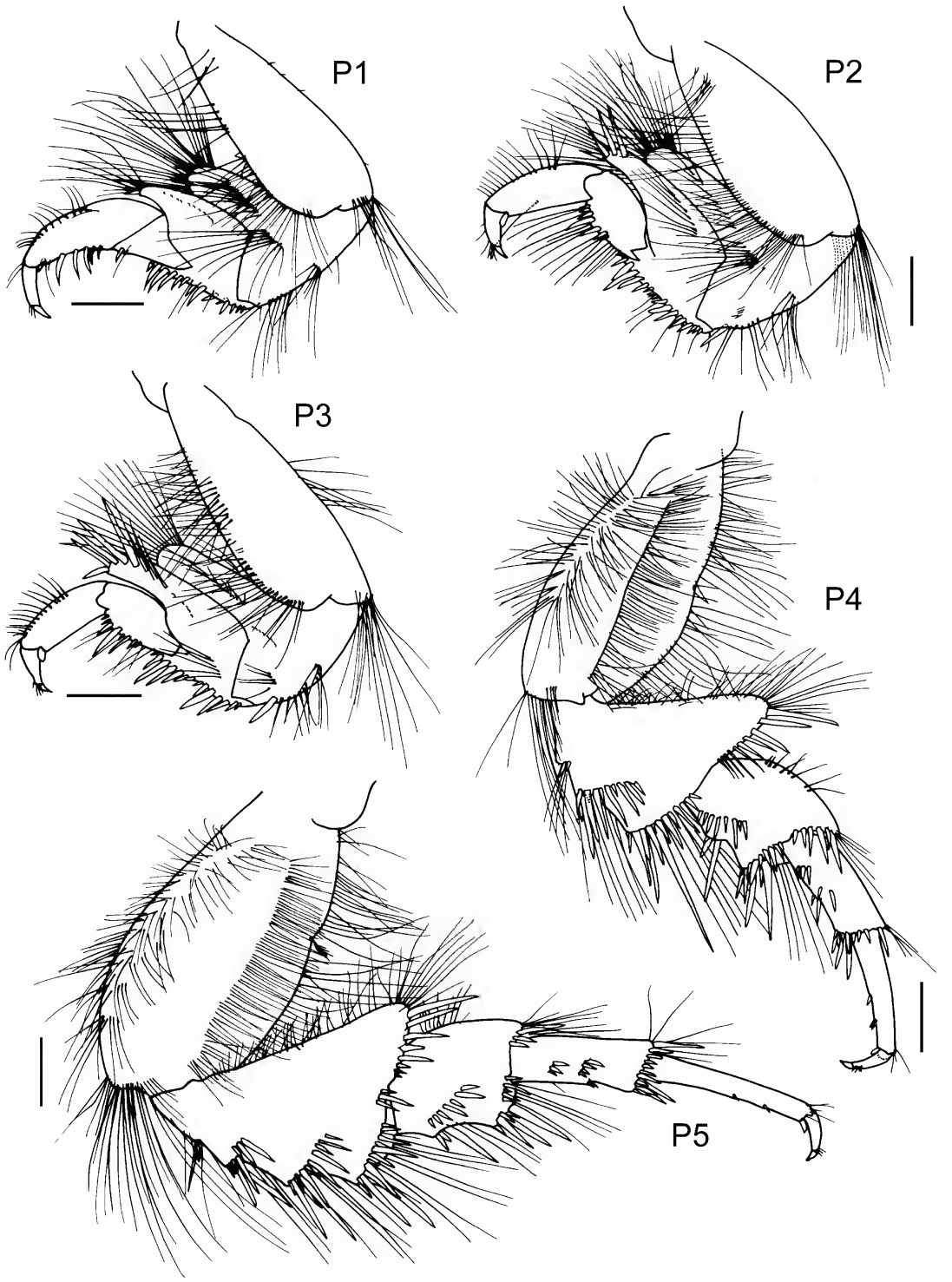

Fig. 18. *Natatolana femina* n.sp., holotype. Scales = 0.5 mm.

of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod triangular; medial margin convex, with 3 RS, PS along entire length; apex with 2 RS; lateral margin straight, with 3 RS, PS along entire length. Exopod medial margin convex, with 4 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 8 RS, PS along entire length.

Supplementary description of male. Based on paratype, 10 mm, AM P47233, not fully mature. *Pleopod 2 appendix masculina*: arising basally.

Variation. The number of robust setae occurring on the pleotelson is variable, the holotype has 15. Among the seven paratype specimens examined in the Tasmanian Museum, three have 14, two have 13, one has 12 and one is damaged.

Sexual dimorphism. In the material examined there was only one male present, this specimen was not fully mature and sexual dimorphism could not be adequately assessed. In mature males of species that may be closely related, however, conspicuously elongate robust setae develop on the carpus of pereopods 1–3 and on the merus of pereopods 4–6.

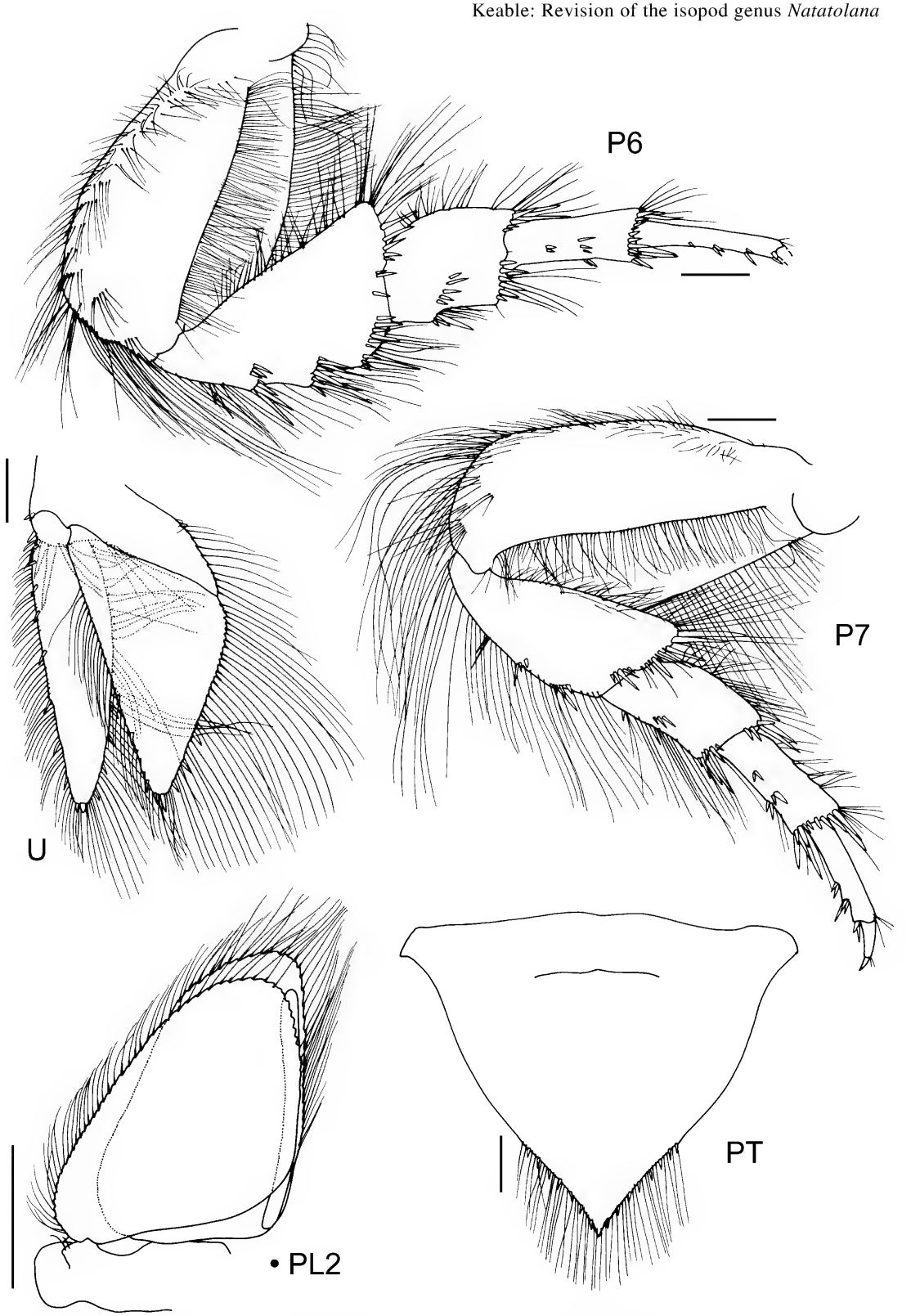

Fig. 19. *Natatolana femina* n.sp., holotype, except; •PL2 = paratype male (immature). Scales = 0.5 mm.

Size. Adults to 25 mm.

Etymology. From the Latin "femine" (the female) in reference to the absence of mature males in the material examined.

Remarks. No fully mature males of *Natatolana femina* are known. Therefore, whether the males develop conspicuously long robust setae on the pereopods as in similar species such as *N. corpulenta* is unclear. Furthermore, the appendix masculina and penes are probably not fully developed in the specimen described here.

Natatolana femina is most similar to *N. natalensis* but differs from that species in having the posterolateral margins of the pleotelson concave (not convex) and in lacking robust setae on the propodal palm of pereopods 2–3. *Natatolana pellucida*, *N. sinuosa* n.sp., *N. debrae* n.sp., *N. corpulenta*

and *N. pallidocula* are also similar. *Natatolana pellucida* differs from *N. femina* in having the posterior margins of coxa 3–4 sinuate, forming weak coxal points at the posteroventral corners of these coxae and because the posterolateral margins of the pleotelson are convex. *Natatolana sinuosa* and *N. debrae* differ from *N. femina* because pereonite 1 and coxae 2–7 have sinuate posterior margins that form strong coxal points at their posteroventral corners in these species. *Natatolana corpulenta* has the anteroventral corner of coxa 2 produced into an acute tooth whereas it is rounded in *N. femina*. *Natatolana pallidocula* has rectangular eyes with 14 ommatidia in the horizontal row whereas in *N. femina* the eyes are rounded with only 5 ommatidia in the horizontal row.

Distribution and ecology. Australia: northeast coast of Tasmania At depths of 5–15 m. Scavenger.

Natatolana flexura n.sp.

Figs. 20–22

Type material. HOLOTYPE: ♂, 6 mm, AM P47222. PARATYPES: All off Wollongong, NSW, baited trap, 100 m, P. Freewater, S. Keable & W. Vader, May 1993; 35 specimens (mancas and ♀♀), AM P47223, 34°28.15'S 151°02.37'E, 15.5°C, SEAS NSW-778; 4♂♂, 18♀♀, 75 mancas, AM P47224, 34°33.41'S 151°21.35'E, SEAS NSW-796. • Type locality: east of Fortescue Bay, north of Hippolyte Rocks, Tasmania, Australia, 43°06.70'S 148°03.45'E, [baited trap], 100 m, [15.8°C, J. Lowry & P. Freewater, 16–17 April 1993, SEAS TAS-355].

Diagnosis. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.82× basal width; anterodorsal depression present; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 2 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.4× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on distal half. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1.07× length of endopod; margins strongly or very strongly curved laterally; broad; apex not at angle to adjacent margins, broadly rounded with a slight depression at tip. *Uropods*: exopod slightly shorter than endopod, 0.81× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.7× width. Colour translucent white with a yellow tinge in alcohol. Chromatophores present; small; yellow to brown in freshly preserved material, fading completely after a short time in preservative; on all sections of the body but concentrated on posterior segments. *Eyes*: with 8 ommatidia in horizontal diameter; with 8 ommatidia in vertical diameter; round; colour red in freshly preserved material, turning to tan after a short time in preservative. Frontal lamina: length c. 4× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta and 2 SS at posterodistal angle, 1 PS and 1 penicillate seta at anterodistal angle; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 3 SS on medial surface, 2 SS and 1 penicillate seta at anterodistal angle; article 5 with 2 large pappose setae at posterodistal angle. Flagellum 16-articulate. *Mandible*: setal row with 18 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 5 SS and 6 PS; middle lobe with 7 long SS on outer row and 2 long SS on inner row. *Maxilliped*: endite with 1 coupling hook, and 3 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1; pereonites 1, 4–5 subequal and longest, 2–3 and 6 subequal and longer than 7. *Coxae*: pereonite 1, coxae 2–3 posteroventral corners rounded, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pleotelson*: posterolateral margins conspicuously serrate. *Pereopod 7*: basis anterior margin slightly convex; medial carina with SS; posterior margin convex, PS present. Ischium anterior margin with non-RS absent; posterior margin without RS, PS present. Merus posterior margin with 3 RS, non-RS absent. Carpus posterior margin with 3 RS, SS absent. Propodus longer than carpus; posterior margin with 5 RS, SS absent. *Penes*: forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture feebly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod triangular; medial margin convex, with 3 RS, PS along entire length; apex with 2 RS; lateral margin slightly concave with a prominent notch, with 1 RS and 1 prominent penicillate seta in notch, PS along entire length (but absent from distal section of notch). Exopod medial margin convex, with 2 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 4 RS, PS along entire length.

Variation. The paratype males do not have the appendix maculina as strongly curved laterally as in the holotype.

Size. Adults to c. 6 mm.

Etymology. From the Latin "flecto" (to bend or curve) in reference to the shape of the pleopod 2 appendix masculina.

Remarks. *Natatolana flexura* can be distinguished from all other species in the genus by the presence of an anterodorsal depression on the pleotelson, the low number of robust setae on the margins of the pleotelson and the shape of the lateral margins of the uropod endopod.

Distribution and ecology. Australia: east of Fortescue Bay, north of Hippolyte Rocks, Tasmania; off Wollongong, New South Wales. At depths of 100 m. Scavenger.

Natatolana galathea Bruce, 1986

Natatolana galathea Bruce, 1986: 86, fig. 58.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♀, ZMUC CRU1692 (examined). • Type locality: Gulf of Carpentaria, Australia, 10°37'S 139°19'E.

Material examined. **Western Australia**: series from North-West Shelf, CSIRO 1983, sled, AM P47135–47138: ♂, 19°56.7'S 117°53.6'E, 41 m, 05-B2-S; 2♂♂, ovigerous ♀, 19°56.4'S 117°53.9'E, 44 m, 03-B2-S; ♂, 5♀♀ (1 ovigerous), manca,

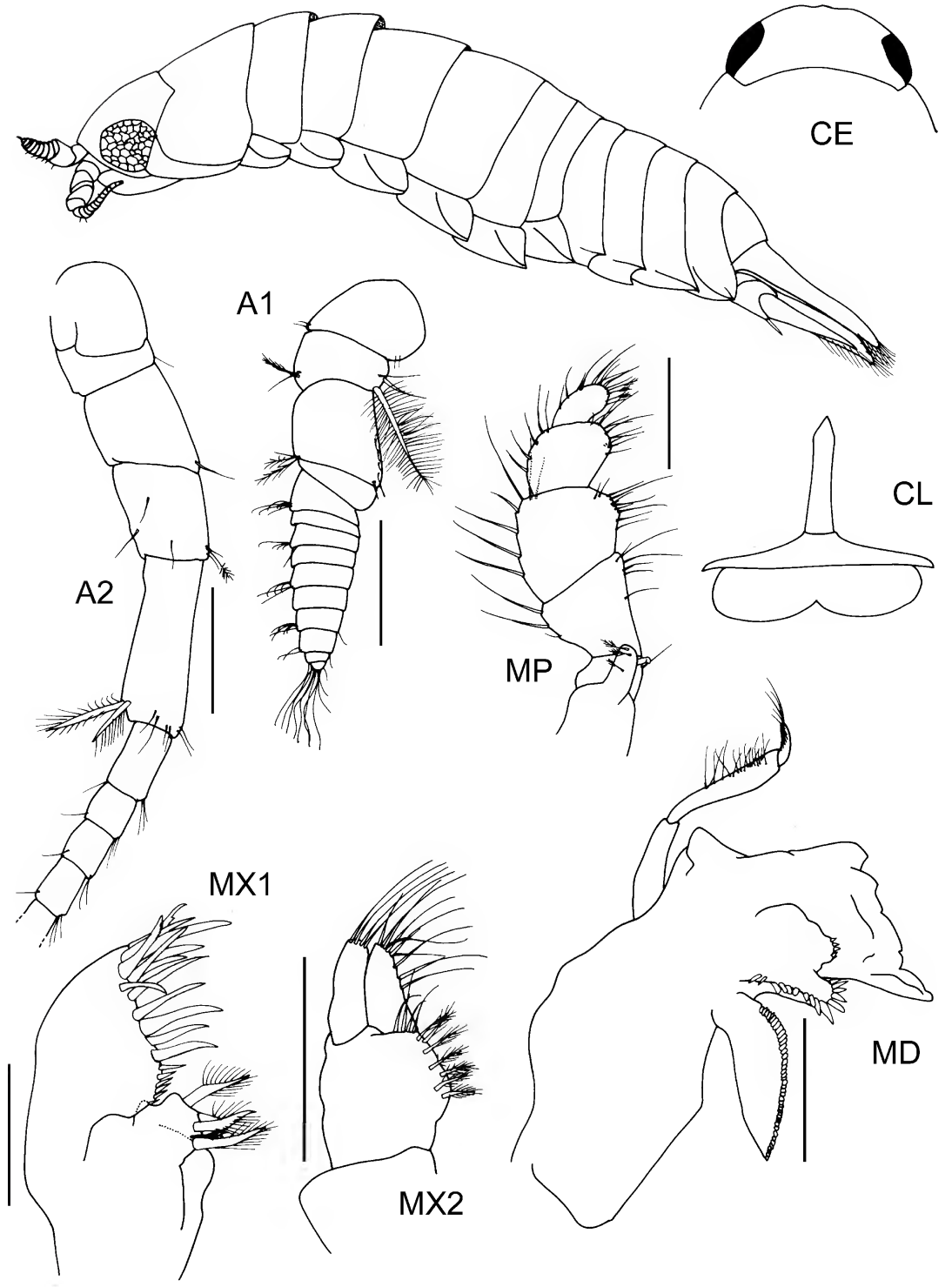

Fig. 20. *Natatolana flexura* n.sp., holotype. Scales = 0.2 mm.

19°56.9'S 117°53.7'E, 42–43 m, 02-B2-S; ♀, 19°59'S 117°51.4'E, 42m, 01-B1-S.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.35× as long as body, reaching to between posterior of pereonite 3 and 4 (not to pereonite 2 as originally described). *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.7× basal width; anterodorsal depression present; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point, or produced into a small point; with 8 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.45× length; distance between anterior margin and medial carina

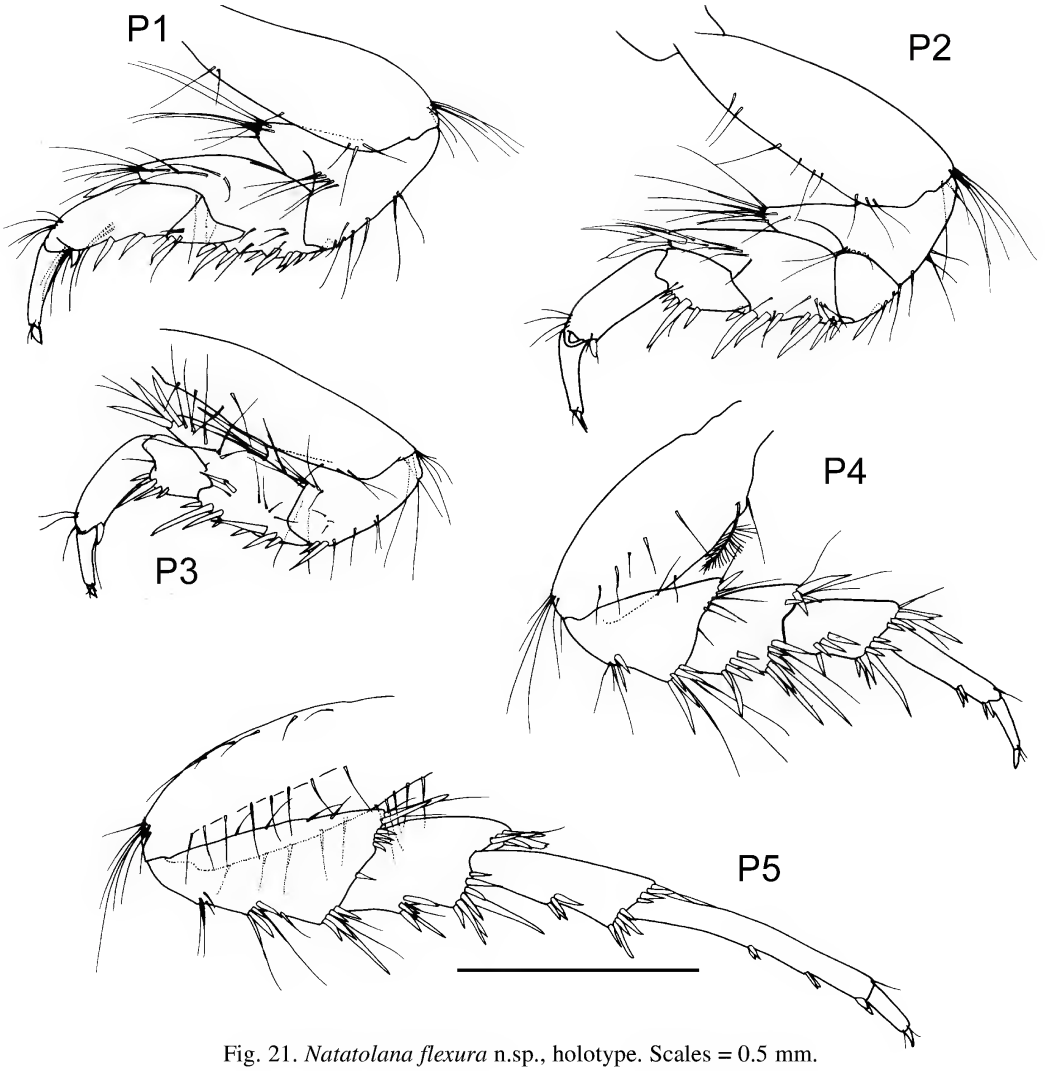

Fig. 21. *Natatolana flexura* n.sp., holotype. Scales = 0.5 mm.

less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; margins strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.85× the length of the endopod.

Sexual dimorphism. Males may have slightly longer antennae, extending to the posterior of pereonite 4. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Adults to c. 7 mm.

Remarks. This is the first record of a male specimen of *Natatolana galathea*. This species is most similar to *N. pellucida* and can be identified by examination of the characters discussed in remarks for that species.

Distribution. Australia: northwestern Western Australia; Gulf of Carpentaria. At depths of 41–57 m.

Natatolana gallica (Hansen, 1905)

Synonymy in Keable & Bruce, 1997: 677, figs. 8–10. Additional listings and records of this species are those of Castelló & Carballo (2001, p. 231).

Type material. Syntypes: 157 specimens, ZMUC CRU147 (examined). • Type locality: Roscoff [France, c. 48°42'N 4°0'W, although Hansen (1905) also cites Guernsey and Jersey as possible type localities and indicates the specimens are from the collections of the maritime station of Roscoff].

Material examined. Listed by Keable & Bruce (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.27× as long as body, reaching to approximately one third of the way along pereonite 3. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.95× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 3–5 RS. *Pereopod 2*: propodus with 0–1 RS on palm. *Pereopod 3*: ischium anterodistal angle produced, but not as produced as on pereopods 1 and 2, similar to pereopod 4. Propodus

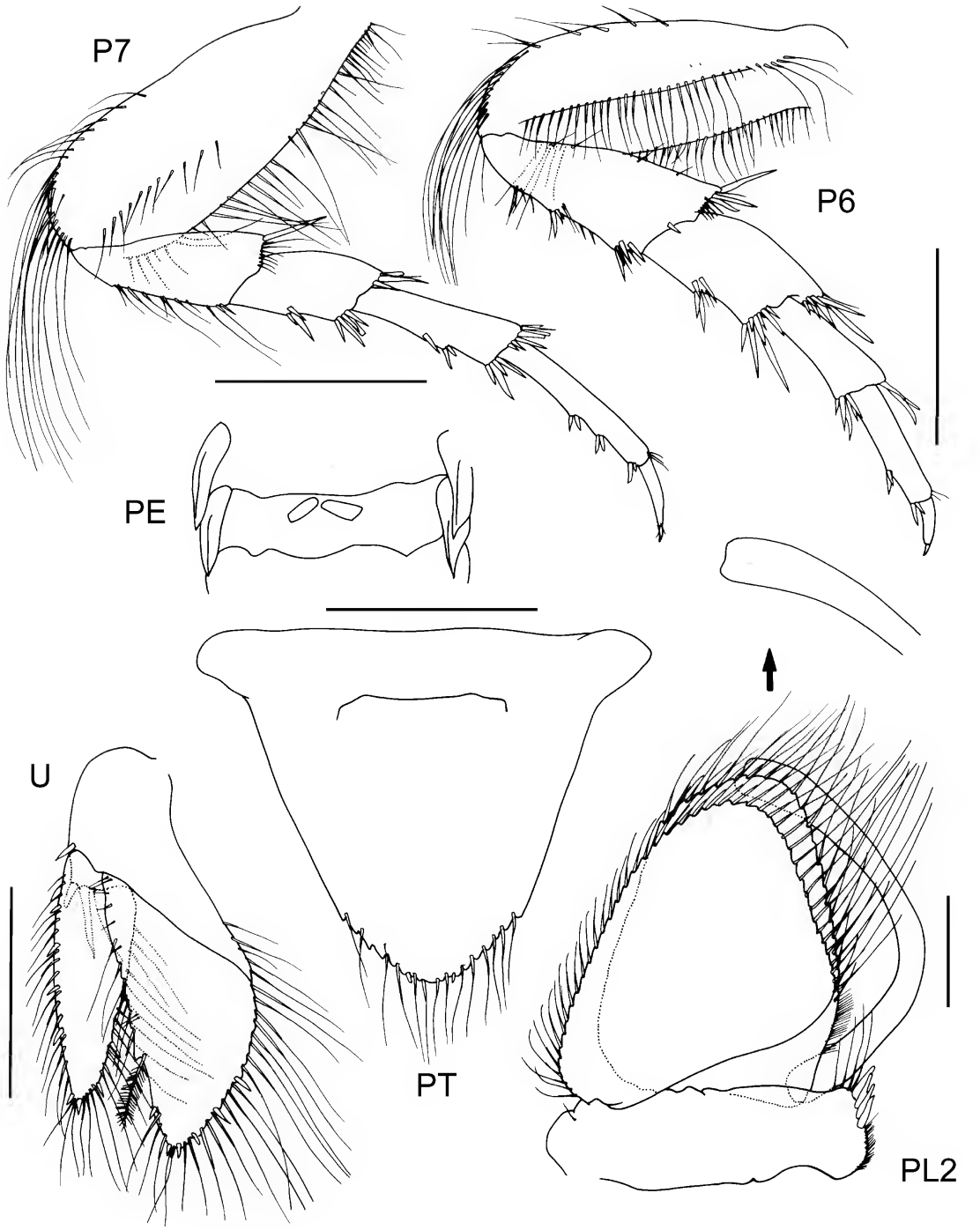

Fig. 22. *Natatolana flexura* n.sp., holotype. Scales = 0.5 mm, except PL2 = 0.2 mm.

with 0–1 RS on palm. *Pereopod 7*: basis broad, width 0.65× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with dense setae along entire length. *Penes*: absent, vasa deferentia opening flush to surface of sternite 7 (area around openings slightly raised but not forming flexible processes). *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.05× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, with a distinct acute projection. *Uropods*: exopod slightly shorter than endopod, 0.88× the length of the endopod.

Size. To c. 25 mm.

Remarks. *Natatolana gallica* was redescribed by Keable & Bruce (1997). It is most similar to *N. thalme* but differs noticeably from that species in having the posterolateral margin of the pleotelson convex and smoothly continuous with the anterolateral margins (angled to the anterolateral margins in *N. thalme*), more strongly developed coxal furrows, dense setae along the length of the posterior margin of the basis of pereopod 7 (sparse in *N. thalme*) and in often having robust setae on the palm of the propodus of pereopods 2 and 3 (absent in *N. thalme*).

Distribution. Atlantic coasts of Europe and northern Africa. At depths of 8–210 m (Keable & Bruce, 1997; Castelló & Carballo, 2001).

Natatolana gorung Bruce, 1986

Natatolana gorung Bruce, 1986: 66, figs. 42, 43.–Springthorpe & Lowry, 1994: 46.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♂, 14.5 mm, NMV J1340 (not examined). Paratype: AM P24324 (examined). • Type locality: Port Phillip Bay, Victoria, Australia, 38°19'S 144°47'E.

Material examined. **New South Wales**: 3 adults, manca, AM P38673, Middle of Spring Cove, North Harbour, Port Jackson, baited trap, 15 m, S. Keable, D. Townsend, J. Lowry, 16–17 Jul. 1988; series from Bate Bay, Pioneer Cement/The Ecology Lab. EIS Study, AM P47277–47281, baited trap, 1991: 100 specimens, S1R1 E deep; 3 specimens, S1R1 deep; 30 specimens, S2R1 deep; 97 specimens (2 vials), S1R2 E deep; same study off Providential Head, 62 m; series from Jervis Bay, CSIRO Baseline Studies, P. Hutchings *et al.* AM, corer, AM P47271–47276; 1 specimen, site 4#5, 25 May, 1990; 1 specimen, site 4#2, 5 Jun. 1990; 5 mancas, site 6#3, Aug. 1989; manca, site 6#2, 5 Jun. 1989; manca, site 4#2, Jun. 1989; manca, site 6, Aug. 1989.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, forming a ridge that runs across the cephalon and deflects anteriorly towards the midpoint. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.25× as long as body, reaching to posterior of pereonite 1. *Coxal plates*: furrows variously developed, strongly developed on pereonite 1 and coxae 2–3, absent on coxae 4–6, weakly developed on coxa 7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.83× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex not produced, lateral margins converging smoothly to a point; with 10–12 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.55× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae proximally and distally but not medially. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.96× length of endopod; slender; margins straight; apex bent laterally slightly, bluntly rounded. *Uropods*: exopod short, 0.75× the length of the endopod.

Size. Adults to 18.6 mm.

Remarks. The incomplete interocular furrow formed into a distinct ridge is sufficient to distinguish *Natatolana gorung* from all other species in the genus.

Distribution and ecology. Australia: New South Wales: Port Jackson; off Sydney; Jervis Bay. Victoria: Port Phillip Bay. To depths of 66 m. Scavenger.

Natatolana gracilis (Hansen, 1890)

Synonymy in Keable & Bruce, 1997: 682, figs. 11–12.

Type material. Holotype: ♂, 8 mm, ZMUC CRU152 (examined). • Type locality: the only type specimen was without location data but Hansen (1890) indicates that there is a high probability that it was collected at St Thomas, Virgin Islands [c. 18°20'N 64°55'W].

Diagnosis. *Eyes*: well developed (Hansen (1890) describes the eyes as large with a few large ommatidia, these have faded in the holotype and are now barely apparent). *Interocular furrow*: absent. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.4–0.5× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.87× basal width; anterodorsal depression absent (although the anterior margin is thickened, and there is a smooth curve to a depression, this is not equivalent to the distinct and abrupt depression found in species such as *N. pellucida*); anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex produced into a small point; with 7–8 RS. *Pereopod 2*: propodus with 4 RS on palm (illustrated by Hansen (1890), pereopod 2 propodus now missing from holotype). *Pereopod 3*: propodus with 3 RS on palm. *Pereopod 7*: basis narrow, width 0.38× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: unknown (the only specimen that can be identified with certainty is damaged and fragile, there appear to be 2 flattened lobes present, these may be penes but because of the fragile nature of the specimen these could not be examined closely enough to conclude that they were penes). *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.07× length of endopod; margins very strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.8× the length of the endopod.

Sexual dimorphism. Based on the record of Koening (1972), females apparently differ from males only in the primary sexual characters and do not have the pleopod 2 appendix masculina. The possibility of further sexual dimorphism, however, is uncertain until samples from the type locality, containing both sexes, have been examined.

Size. Only measured specimen reported is 8 mm.

Remarks. The most distinctive feature of *Natatolana gracilis* is the shape of the male appendix masculina. The holotype is the only male specimen that has been reported and is, therefore, the only specimen that can be attributed to the species with certainty. Further specimens from the vicinity of the type locality are needed in order to expand upon the redescription of Keable & Bruce (1997).

Distribution. The type locality is uncertain but is probably St Thomas, U.S. Virgin Islands. Also reported from northern Brazil at depths of 7–85 m (Koening, 1972; Pires-Vanin, 1998) but this requires verification (Keable & Bruce, 1997).

Natatolana helenae n.sp.

Figs. 23–24

Type material. HOLOTYPE: ♂, 14 mm, QM W18851. • Type locality: Gulf of Carpentaria, Australia, 10°41.4'S 141°51.6'E, [grab], 10 m, [CSIRO Southern Surveyor, 29 Nov. 1991, stn 62].

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.8× as long as body, reaching to posterior of pereonite 6. *Coxal plates*: furrows moderately developed, on all coxae.

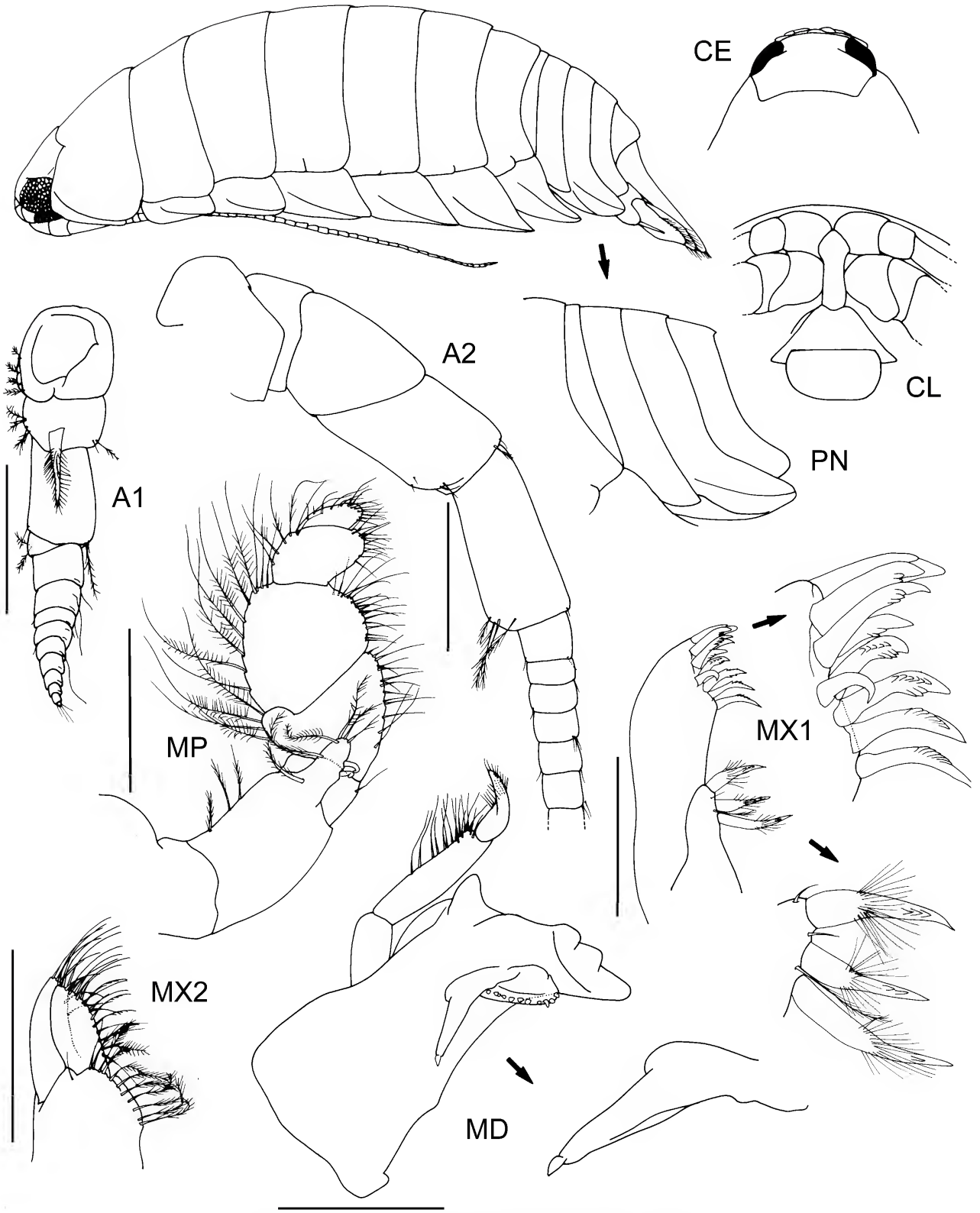

Fig. 23. *Natatolana helenae* n.sp., holotype. Scales = 0.5 mm.

Pleonite 2: ventral posterolateral margin not produced. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.67× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, contiguous with anterolateral margins; apex truncate with a serrate margin; with 8 RS. *Pereopod 2*: propodus without RS on palm. *Pereopod 3*: ischium anterodistal angle produced subequal to pereopod 2, both more produced than pereopod 1 ischium. Propodus without RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.61× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior

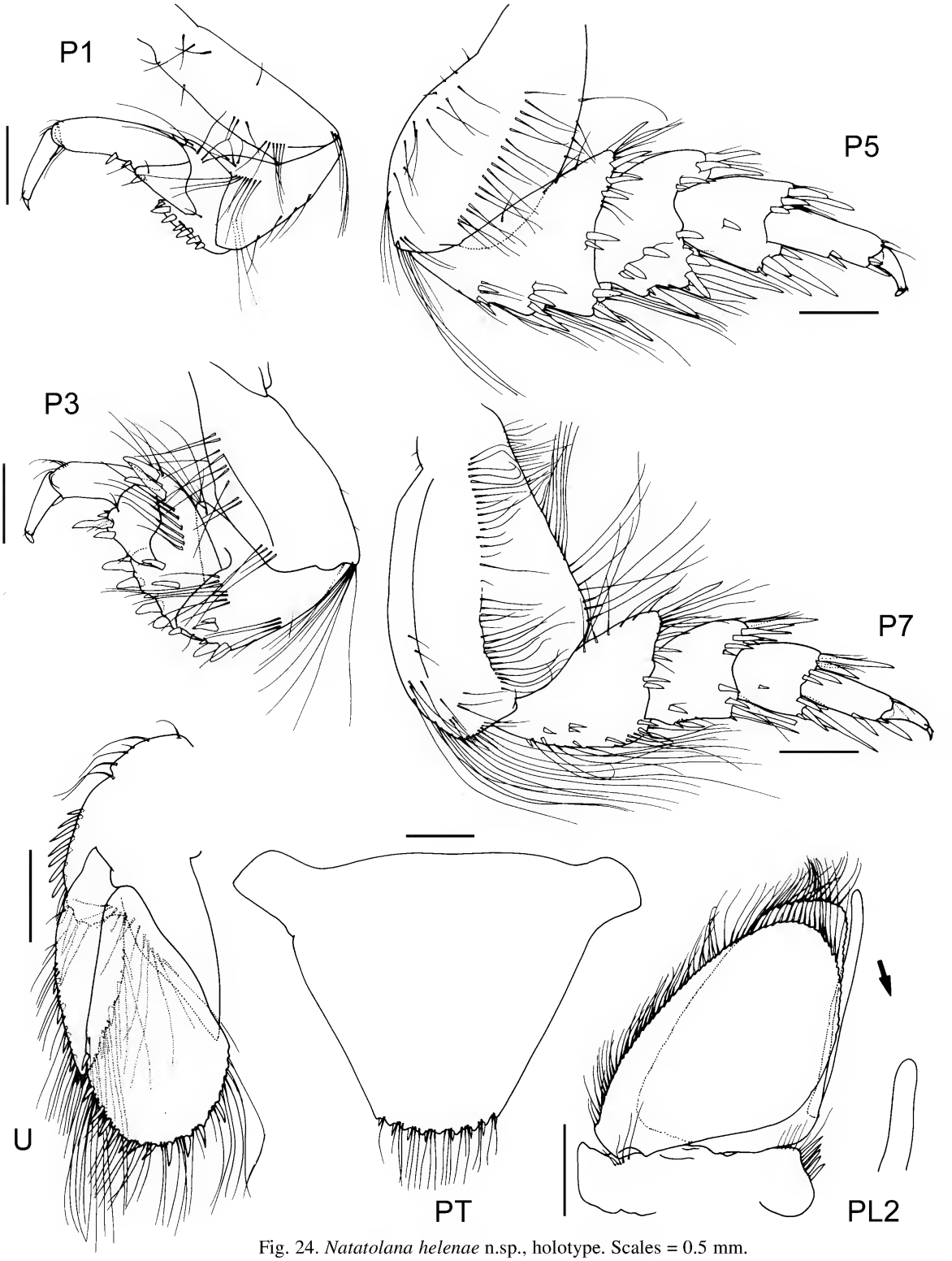

Fig. 24. *Natatolana helenae* n.sp., holotype. Scales = 0.5 mm.

margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.08× length of endopod; margins straight; slender; apex bent laterally slightly, bluntly rounded. *Uropods*: exopod short, 0.73× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.35× width. Colour cream in alcohol. Chromatophores absent. *Eyes*: with 9 ommatidia in horizontal diameter; with 6 ommatidia in vertical diameter; ovate; colour tan in alcohol. *Frontal lamina*: length c. 3× basal width; apex expanded, anterior margin angled. *Antennule*: short, just reaching pereonite 1. Peduncular article 1 longer than article 2; article 2 with 1 large pappose seta medially and several penicillate setae on margins; article 3 short, subequal to article 1. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 4 short SS at posterodistal angle, 1 penicillate and 1 short SS at anterodistal angle;

article 5 with 3 pappose setae and 1 SS at posterodistal angle. Flagellum 47-articulate. *Mandible*: molar RS absent on margins; incisor narrow, with posterior tooth not strongly developed; setal row with 11 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae (larger setae with serrations), lateral margin with protuberance absent; lateral lobe with 11 RS on distal surface. *Maxilla*: lateral lobe with 8 SS (2 are uniserrate and 3 are biserrate); medial lobe with 3 SS and 9 PS; middle lobe with 18 SS, 7 of which are serrate. *Maxilliped*: palp lateral margin with PS on most of the length of articles 2–5; article 5 serrate setae absent. Endite with 2 coupling hooks, and 6 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–7; pereonite 1 longest, 2–5 subequal, 6–7 progressively shorter. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–6 with increasingly produced, broad, acute posteroventral corners, coxa 7 posterior margin distinctly concave and posteroventral corner produced into a narrow acute point. *Pleonite 2*: dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin. *Pleonite 3*: rounded. *Pleotelson*: PS restricted to apex. *Pereopod 1*: propodus posterodistal angle without RS opposing dactylus. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex. Ischium broad, width greater than length; anterior margin with SS; posterior margin with 5 RS (and 3 submarginally), PS present. Merus posterior margin with 2 RS (and 1 submarginally), SS present. Carpus posterior margin without RS, SS absent. Propodus subequal to carpus; posterior margin with 2 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod subcircular; medial margin rounded, with 4 RS, PS along entire length; apex with 3 RS; lateral margin straight for proximal two thirds, convex at distal third, with 5 RS and 1 penicillate seta, PS on distal third. Exopod medial margin convex, with 3 RS, PS on distal three-quarters; apex acute, with 3 RS; lateral margin convex, with 4 RS, PS on distal two-thirds.

Size. Adults to 14 mm.

Etymology. Named after Ms Helen Stoddart, in recognition of the help she has given me in this and other studies.

Remarks. *Natatolana helenae* is distinguished from all others species in the genus by the truncate, serrate pleotelson. The lack of robust setae on the mandible molar, the presence of plumose setae on the lateral margins of the maxilliped palp, the serrations on the pappose setae of the medial lobe of the maxillule and the absence of a robust seta at the posterodistal angle of the pereopod 1 propodus, are also unique characters within the genus.

Distribution. Australia: known only from Gulf of Carpentaria. In a depth of 10 m.

Natatolana hirtipes (Milne Edwards, 1840)

Figs. 25–28

Cirolana hirtipes Milne Edwards, 1840: 236, pl. 31, figs. 25, 26.–Milne Edwards, 1836–49 [exact publication date unknown, see Sherborn (1922), subsequent to Milne Edwards (1840)]: pl. 67, figs. 6–6i.–Hansen, 1890: 326, pl.1, figs. 2–2g.–Stebbing, 1910: 421.–Tattersall, 1913: 880.–Vanhöffen, 1914: 501, fig. 38.–?Barnard, 1936: 150.–Kensley, 1975: 39.–1978: 67, fig. 27 E–F.–Huber, 1992: 58.

Natatolana hirtipes.–Bruce, 1981: 957, 958.–1986: 53, 97, 222.–Brusca *et al.*, 1995: 80.–Kensley, 2001: 230.

Not *Cirolana hirtipes*.–Heller, 1866: 742.–Stalio, 1877: 1375.–Stossich, 1880: 224 [mis-identification = *Natatolana neglecta* (Hansen, 1890)].

Not *Cirolana hirtipes*.–Goss, 1855: 133.–White, 1857.–Lo Bianco, 1903: 258 [mis-identification = *Natatolana borealis* (Liljeborg, 1851)].

Not *Cirolana hirtipes*.–Filhol, 1885: 445, 449, pl. 53 fig. 6.–Nierstrasz, 1931: 158.–Hurley, 1961: 267 [mis-identification = *Natatolana rossi* (Miers, 1876)].

Type material. Lectotype: designated here, ♂, 24 mm, MNHN Is. 96. Paralectotype: ♀, 27 mm, MNHN Is. 96. All examined. • Type locality: Cape of Good Hope (as Cap de Bonne-Esperance), South Africa, [34°22'S 18°30'E].

Material examined. **South Africa**: ♂, 18 mm, ♀, 12 mm and manca, 10 mm, SAM-A14579, False Bay, FAL 587 G–E; 11 ♂♂, 6♀♀, ZMUC CRU160, Table Bay, Swedish South African Expedition, 1935, Zool. Inst. Lund. (Prof. O. Carlgren) ded. 1-7-1937; ♂, ZMUC CRU161, Table Bay [as Tafel Bay], Strandgaard, Studiesaml [teaching collection], ded. 1890, 23-5-1890.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4× as long as body, reaching to just beyond the posterior of pereonite 3 (i.e., about ¼ of the way along pereonite 4) or the posterior of pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.82× basal width; anterodorsal depression absent; anterolateral margins convex (in type material), or almost straight and angling posteriorly toward midline; posterolateral margins convex (in type material), or straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex not produced, lateral margins converging smoothly to a point; with 12–19 RS (18 in lectotype). *Pereopod 2*: propodus with 1 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis broad, width 0.54× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal quarter. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.98× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.98× the length of the endopod.

Additional descriptive characters. Based on the type material, the female paralectotype was used for the whole animal illustration and was checked against the male lectotype that had been slightly squashed, the lectotype was used for all dissected parts. *Body*: length c. 3× width. Colour translucent cream-white in alcohol. Chromatophores absent. *Eyes*: with

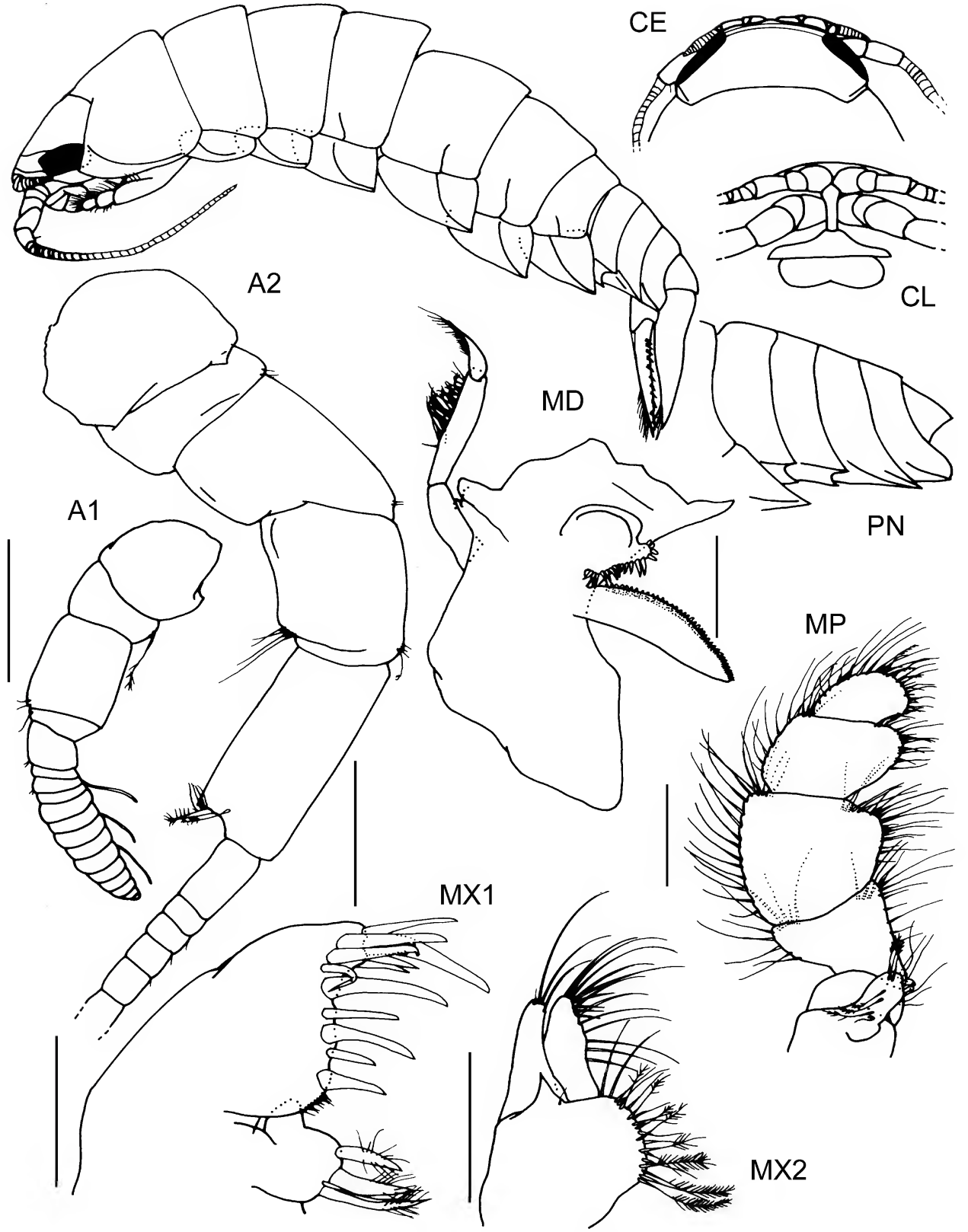

Fig. 25. *Natatolana hirtipes*. Whole animal = paralectotype female, all other parts = lectotype male. Scales = 0.5 mm.

14 ommatidia in horizontal diameter; with 10 ommatidia in vertical diameter; rectangular; colour tan in alcohol. *Frontal lamina*: length c. 4× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 long narrow pappose seta; article 3 short, subequal to article 1. Flagellum 14-articulate. *Antenna*: peduncular article 4 with 4 SS at posterodistal angle and 1 penicillate seta at anterodistal angle; article 5 with 1 pappose seta and 1 penicillate seta at posterodistal angle. Flagellum 35-articulate. *Mandible*: setal row with 17 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 12 RS on distal surface. *Maxilla*: lateral lobe

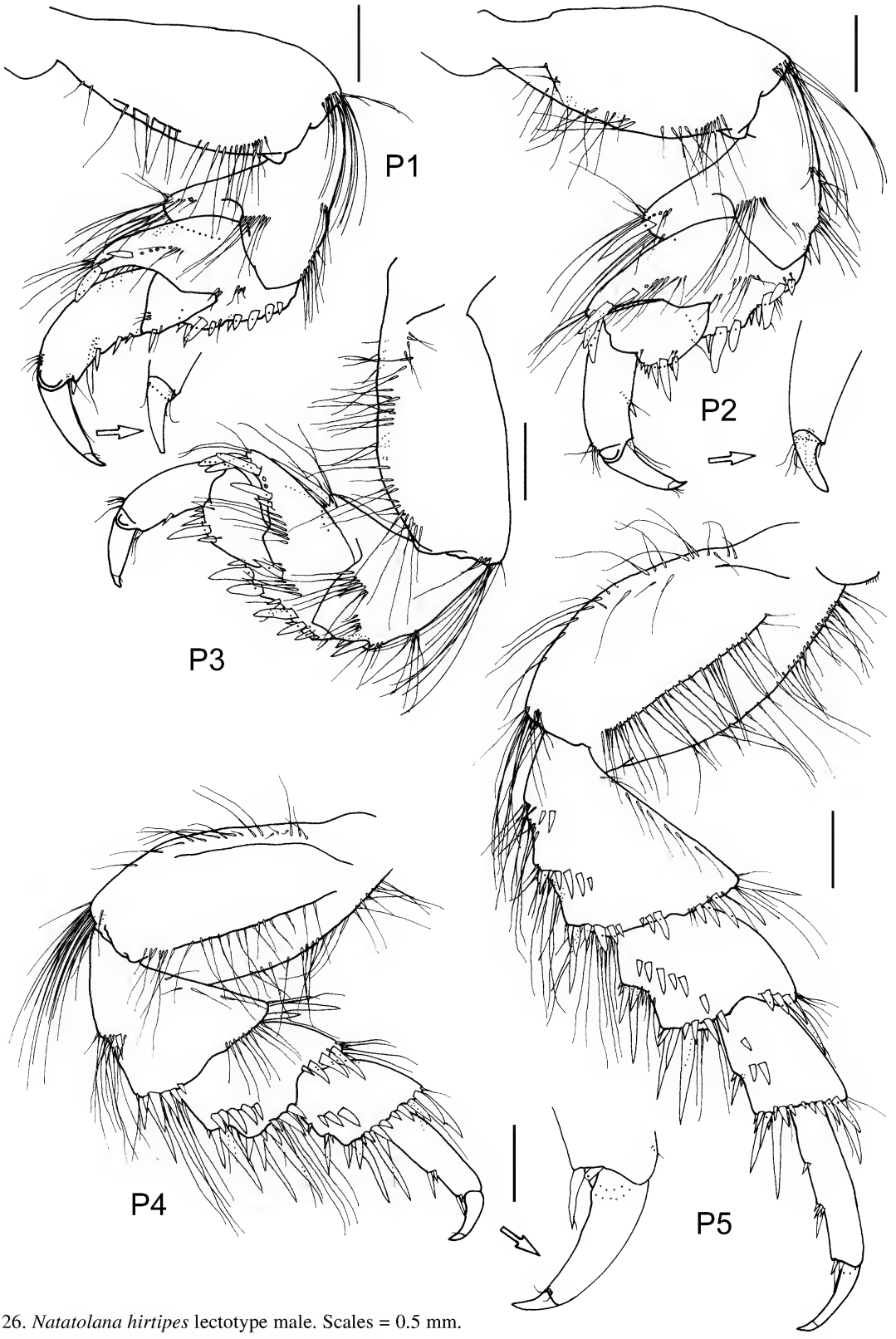

Fig. 26. *Natatolana hirtipes* lectotype male. Scales = 0.5 mm.

with 4 SS (one of which is broken); medial lobe with 11 SS and 9 PS; middle lobe with 16 SS. *Maxilliped*: endite with 2 coupling hooks, and 7 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on the lateral margin of pereonite 1 and 1 short, medial furrow on the lateral margins of pereonites 4–7; pereonites 1 and 5 subequal in length and longest, 2–4 and 6 subequal and longer than 7. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin sinuate; medial carina with PS and SS present; posterior margin

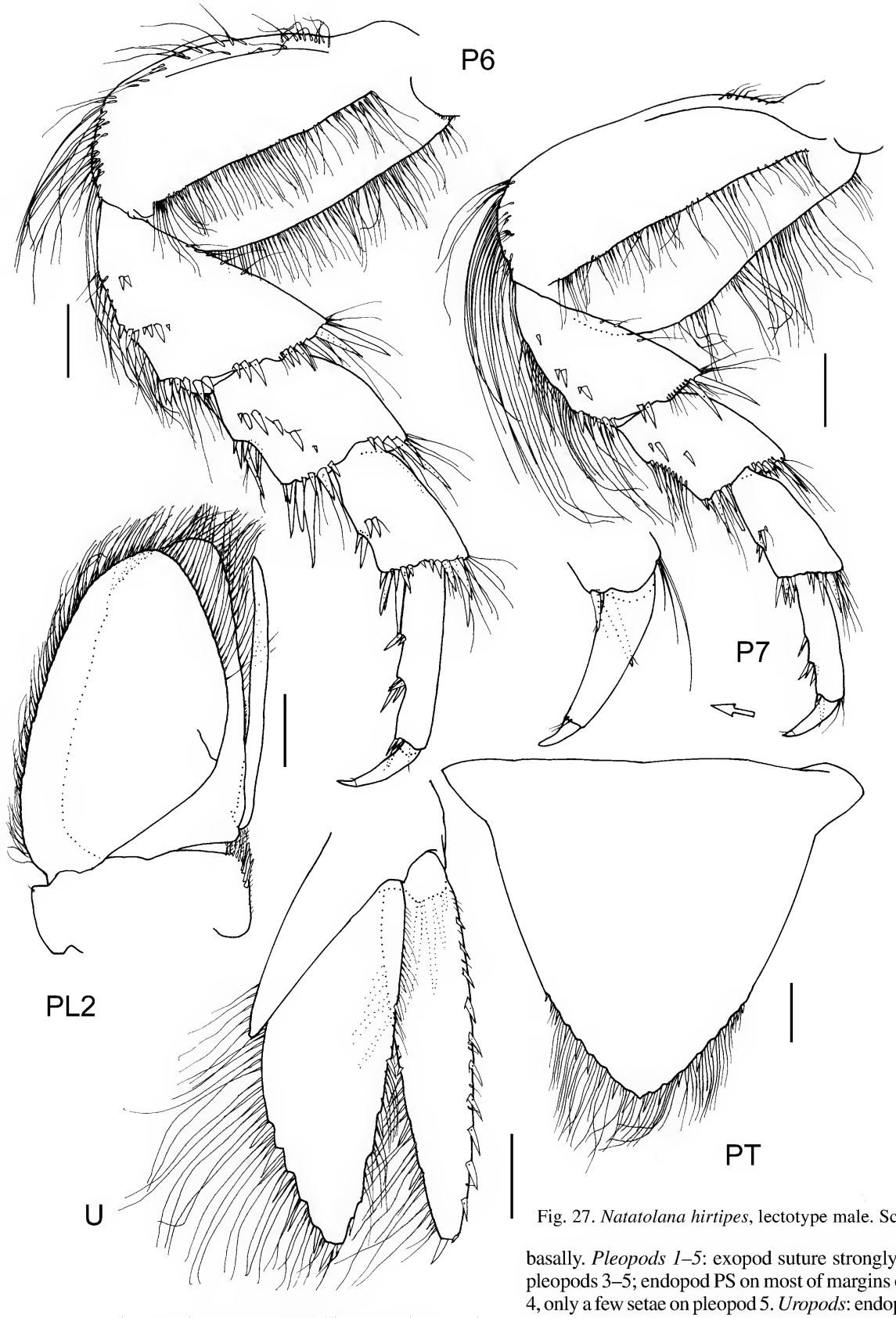

Fig. 27. *Natatolana hirtipes*, lectotype male. Scales = 0.5 mm.

convex, posterior margin PS present. Ischium anterior margin with SS (sparse); posterior margin with 5 RS (submarginal), PS and SS present. Merus posterior margin with 3 RS (submarginal), SS present. Carpus posterior margin with 4 RS, SS absent. Propodus subequal to carpus; posterior margin with 5 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 6 RS, PS along entire length. Exopod medial margin convex, with 3 RS, PS on distal three-quarters; apex acute, with 2 RS; lateral margin convex, with 10 RS, PS along entire length (although most have been broken or been rubbed off).

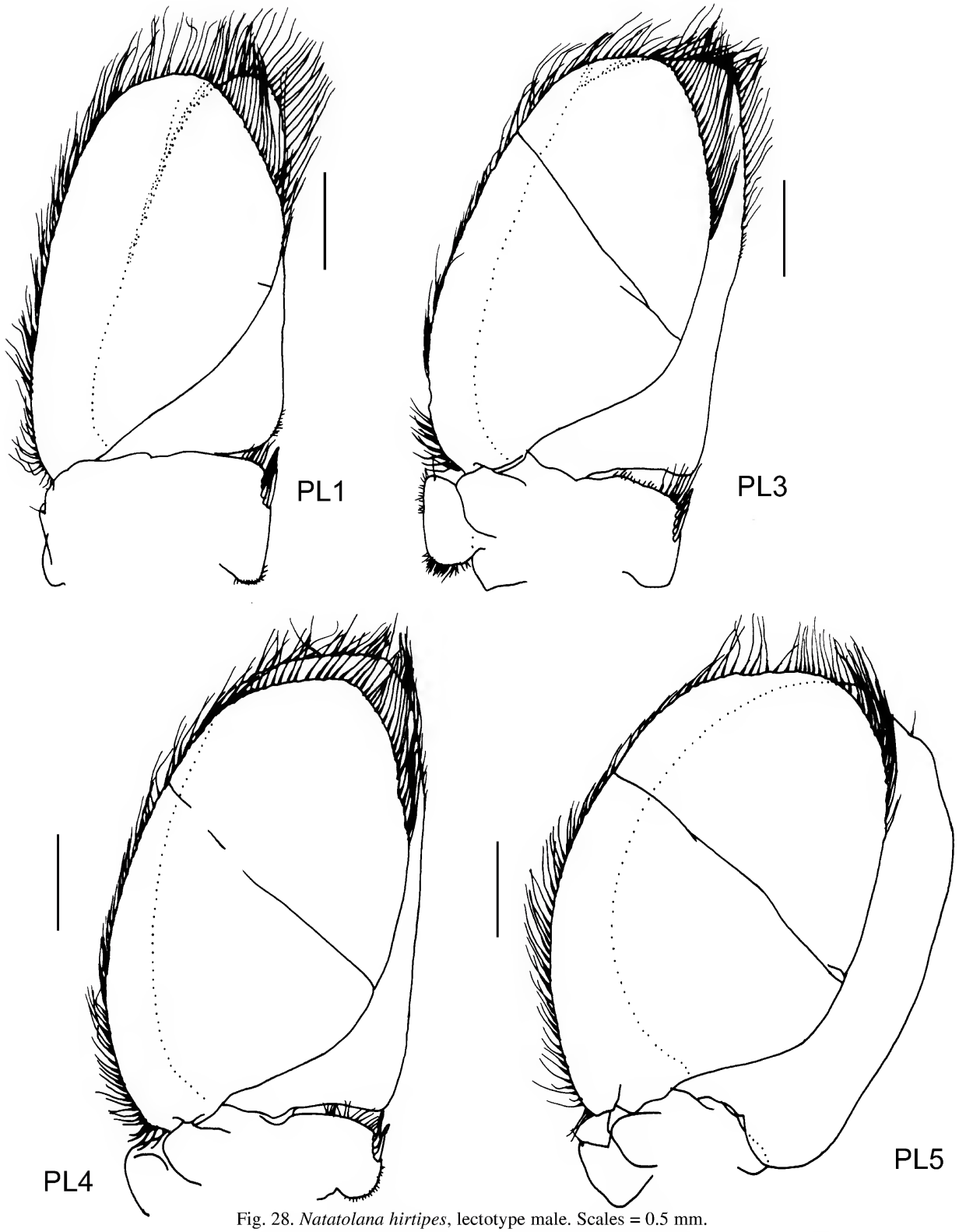

Fig. 28. *Natatolana hirtipes*, lectotype male. Scales = 0.5 mm.

Variation. The male lectotype has pleonite 1 clearly visible between pereonite 7 and pleonite 2, in the female paralectotype pleonite 1 is just visible. The male, female and manca specimens from False Bay (SAM A-14579) all have pleonite 1 just visible. On these non-type specimens the antennae reach the posterior of pereonite 4 (not just beyond the posterior of pereonite 3 as in the types) and smaller specimens have fewer articles in the antennal flagellum. Seventeen specimens from Table Bay (ZMUC CRU160) were also examined for variations in the numbers of robust setae occurring on the pleotelson and uropods. These robust setae are quite long in *Natatolana hirtipes* and appear to be readily dislodged from the animals, resulting in considerable variation between specimens as the setae regenerate. Also, robust setal counts on the pleotelson and uropods often varied from one side of a specimen to the

other. These counts showed no correlation with the size of the animal, small specimens occasionally having more setae than large specimens. The male lectotype has 18 robust setae on the pleotelson. Variations in the number of robust setae present, were as follows: on the pleotelson, ranged from 12–19 (average 14, 40%); on the uropod endopod medial margin, ranged from 4–6 (average 5, 59%); on the uropod endopod apex 2 were present (or sockets indicated their presence) in all specimens; on the uropod endopod lateral margin, ranged from 5–8 (average 7, 35%); on the uropod exopod medial margin ranged from 1–4 (average 3, 53%); on the uropod exopod apex 2 were present (or sockets indicated their presence) in all specimens; on the uropod exopod lateral margin, ranged from 8–14 (average 10, 29%). The specimens examined from Table Bay (ZMUC CRU160, ZMUC CRU161) all have 5 pleonites clearly visible. Males in ZMUC CRU160 all have two indistinct tubercles dorsally on the surface of pereonite 2, however, these are not discernible in the type material. Some specimens in ZMUC CRU160 also have the pleotelson margins straighter and more angular than in the type material. Hansen (1890) described the specimen ZMUC (CRU161) (20 mm in length) from Table Bay, this specimen has 18 robust setae on the pleotelson and an antennal flagellum with 35 articles but is otherwise indistinguishable from the lectotype of *N. hirtipes*.

Sexual dimorphism. Large males (greater than 24 mm) may have two closely spaced, indistinct tubercles, medially on the dorsal surface of pereonite 2.

Size. Hansen (1890) and Kensley (1978) record lengths of 20 mm. Milne Edwards (1840) states a length of 1 pouce, i.e., 25 mm. The paralectotype female (newly measured) is c. 27 mm. A manca of 10 mm and a female of 12 mm were also examined here.

Remarks. Because *Natatolana hirtipes* is the type species of the genus and, as it shows some variation and may be difficult to separate from other species the male syntype is illustrated, redescribed and designated as a lectotype. The purpose of this is to avoid future taxonomic confusion in applying the generic name and identifying the species. The female syntype becomes a paralectotype.

The type specimens of *Natatolana hirtipes* match the few features discernible in the brief original description and two illustrations of Milne Edwards (1840). Figure 26 of Milne Edwards is misleading, however, showing the antennal peduncle as longer than the flagellum. This is not the case, the flagellum was probably foreshortened in the original illustration.

Natatolana hirtipes is extremely similar to *N. rossi* in most features, as noted by Chilton (1909). Consistent differences between *N. hirtipes* and *N. rossi* include a smoothly convex interocular furrow (medially produced in *N. rossi*), a angled anterior margin to the eye (convex in *N. rossi*), a convex ventral margin to the cephalon (concave in *N. rossi*) and a slightly more sinuate anterior margin of the basis of pereopod 7 in *N. hirtipes*.

Natatolana hirtipes is also similar to *N. matong*. The development of the coxal furrows does not reliably separate the two species as suggested by Bruce (1986).The shape of pleonite 4 is, however, consistently different, *N. hirtipes* having a more sinuate posterodorsal margin. The interocular furrow is smoothly convex and the basis of pereopod 7 basis is also broader in *N. hirtipes*.

Distribution and ecology. South Africa: Luderitz to East London. Intertidal to 200 m depth (Kensley 1978; Bruce 1986). Hansen (1890, 1905) assigned earlier records from the Adriatic Sea to *Natatolana neglecta* and from the Mediterranean Sea to *N. borealis*. The records of *N. hirtipes* by Filhol (1885), also listed by Nierstrasz (1931) and Hurley (1961), from Cook Strait, New Zealand, were considered to be a mis-identification of *N. rossi* by Barnard (1936) who additionally noted that the two species are very similar. Barnard (1936) also recorded a female specimen, 13.5 mm, from the Strait of Hormuz (as Strait of Ormuz), Persian Gulf, and an immature specimen, 8.5 mm, from west of Mangalore, southwest India. He also doubtfully recorded a male specimen of 6 mm from off Southern Myanmar (Burma). These records have not been included in the distribution reported by Kensley (1978) or Bruce (1986) and the material was not examined in this study.

Vanhöffen (1914) reported specimens from Simonstown that were apparently scavenging, along with ostracods, on fish caught in nets.

Natatolana honu n.sp.

Figs. 29–30

Type material. HOLOTYPE: ♂, 11 mm, NIWA 18745. PARATYPES: all off the west coast of the North Island, New Zealand: ♂, 4♀♀, manca, NIWA 18746, 38°30'S 172°24'E, 1244–1245 m, NIWA E904; 5♂♂, 8♀♀, 3 mancas, NIWA 18747, 35°20'S 172°15'E, 1286–1313 m, NIWA E881. • Type locality: off the west coast of the South Island, New Zealand, 42°23.7'S 169°11.8'E, [anchor-box dredge], sand-silt-clay, 1120 m, [P.K. Probert, 22 Feb. 1982].

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, extending across the cephalon or weakly developed, indistinct and not extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.36× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed, absent on coxae 2–5, weakly developed on coxae 6–7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.98× basal width; anterodorsal depression absent (there is a slight depression but it is not as distinct and abrupt as the depression found in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 10–14 RS. *Pereopod 2*: propodus with 1 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.33× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on distal half. *Penes*: present. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.96× length of endopod; margins very strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: endopod lateral margin with prominent excision. Exopod short, 0.77× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.95× width. Colour translucent white in alcohol. Chromatophores absent. *Eyes*: with c. 6 ommatidia in horizontal diameter; with 6 ommatidia in vertical diameter; round; without pigment, ommatidia indistinct in alcohol. *Frontal lamina*: length c. 3.75× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose

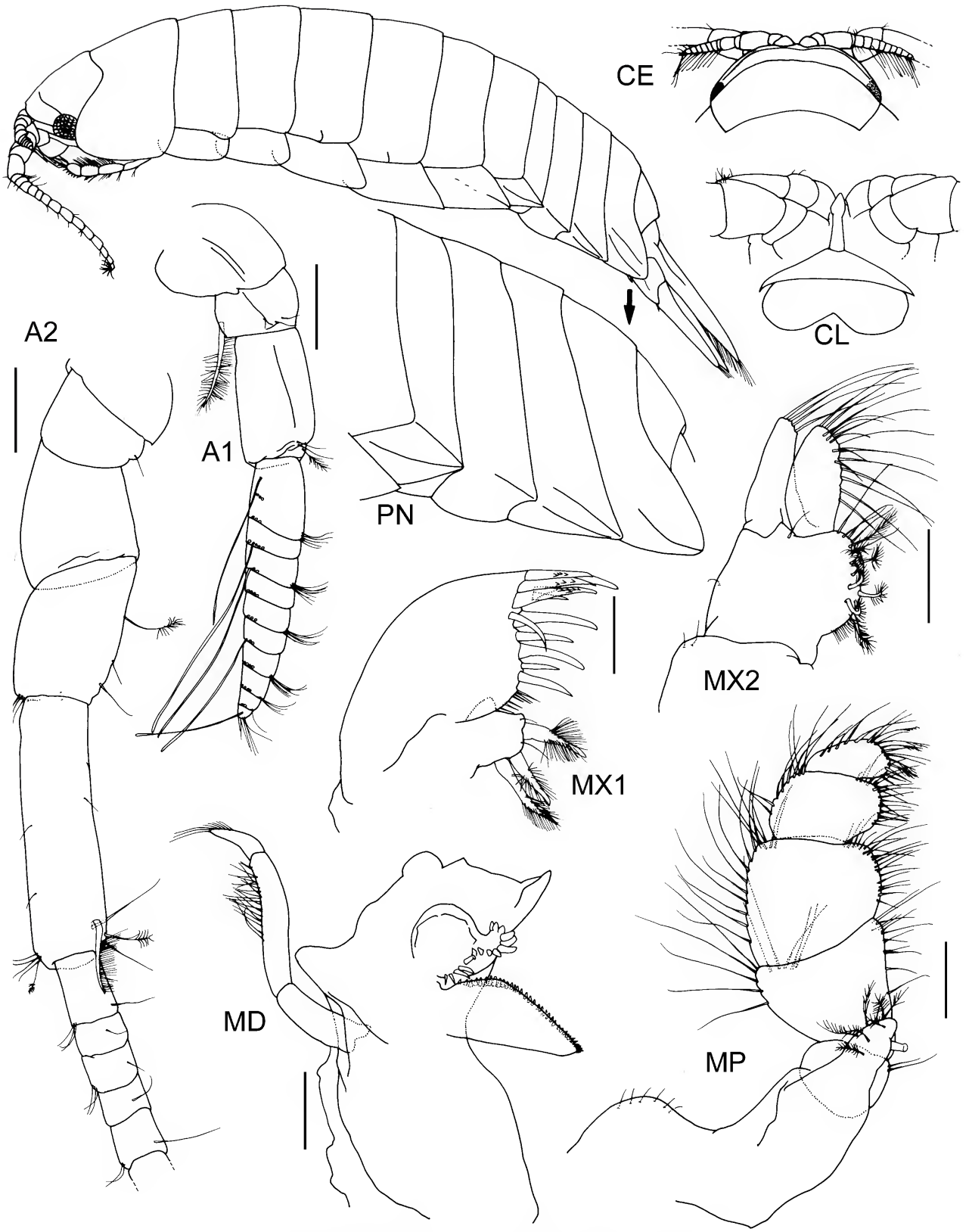

Fig. 29. *Natatolana honu*, n.sp., holotype. Scales = 0.2 mm.

seta; article 3 very long, subequal to or longer than the combined lengths of articles 1 and 2. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 1 penicillate seta and 2 SS on posterior margin, 3 SS at anterodistal angle; article 5 with 1 pappose, 1 penicillate and 2 SS at posterodistal angle, 4 SS and 1 penicillate seta at anterodistal angle. Flagellum 21-articulate. *Mandible*: setal row with 15 RS. *Maxillule*: medial lobe with 3 large robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 6 SS and 9 PS; middle lobe with 1 medial row of 5 SS, 1 lateral row of 11 SS. *Maxilliped*: endite with 1 coupling hook, 7 PS and 1

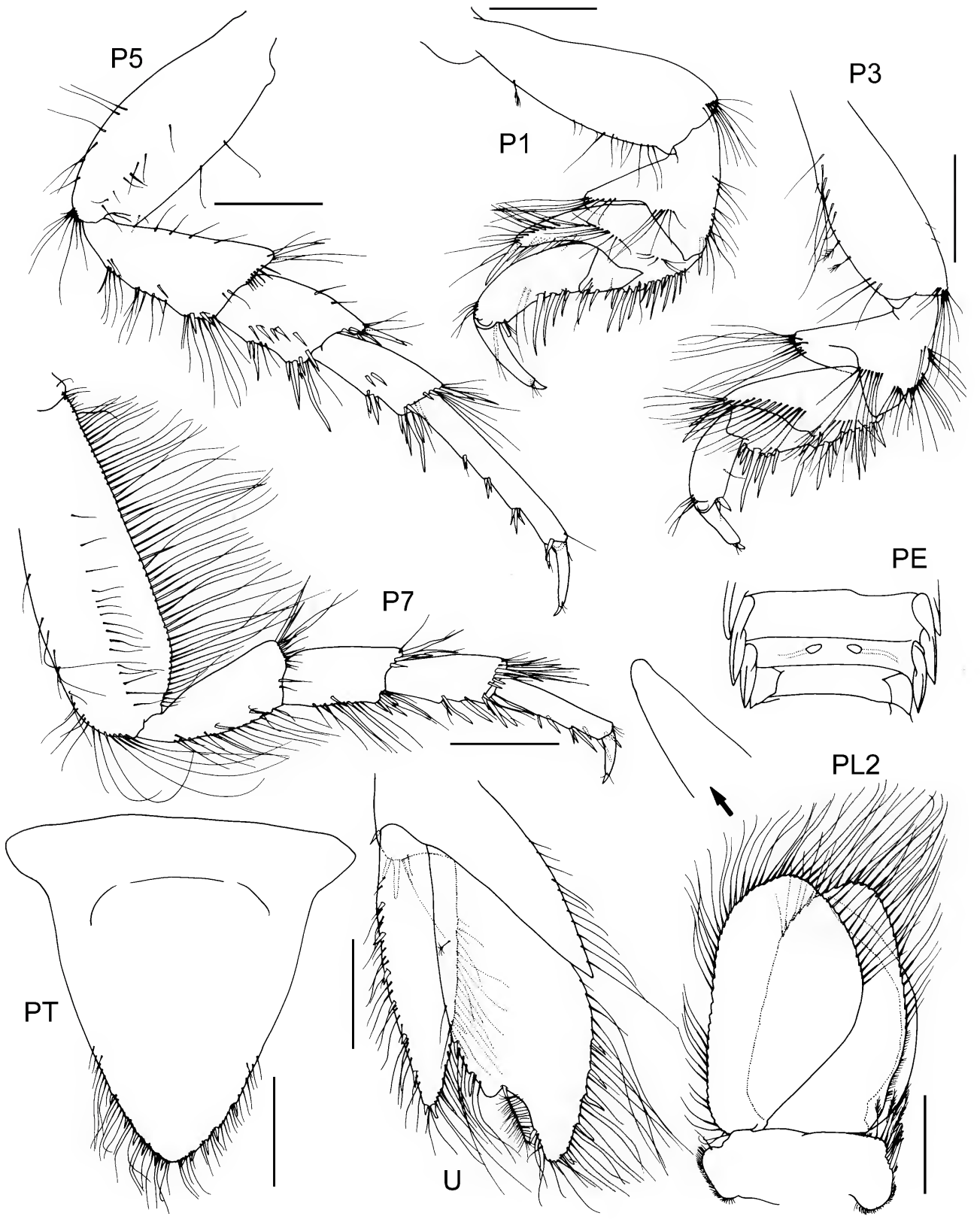

Fig. 30. *Natatolana honu*, n.sp., holotype. Scales = 0.5 mm.

SS. *Pereon*: ornamentation absent, all pereonites smooth; pereonite 1 longest, 2–6 subequal, 7 shortest. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin. *Pereopod 7*: basis anterior margin straight; medial carina with SS (on distal three quarters); posterior margin convex, SS present. Ischium anterior margin with non-RS absent; posterior margin with 2 RS (submarginal), PS

present. Merus posterior margin with 1 RS (submarginal), SS present. Carpus posterior margin with 4 RS, SS present. Propodus longer than carpus; posterior margin with 6 RS, SS absent. *Penes*: forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex with a prominent lateral excision near apex, with 3 RS, 1 conspicuous penicillate seta in excision, PS on distal third (but absent from proximal part of excision). Exopod medial margin convex, with 3 RS, PS on distal three quarters; apex acute, with 2 RS; lateral margin convex, with 6 RS, PS on distal three quarters.

Variation. The holotype has 11 robust setae on the pleotelson. It is difficult to ascertain the usual number of robust setae present on the pleotelson, as these have been rubbed off most of the material available, but it appears to range between 10 and 14. In some specimens, the interocular furrow is indistinct and incomplete.

Size. Adults to 16.5 mm.

Etymology. From the Maori for deep, in reference to the depths the type specimens have been recorded from.

Remarks. *Natatolana honu* and *N. variguberna* are the only species of *Natatolana* with a prominent excision near the apex of the uropod endopod lateral margin. *Natatolana honu* most noticeably differs from *N. variguberna* in having vestigial rather than well-developed eyes, coxal furrows only on the posterior coxae, penes in males, and a greater number of robust setae on the pleotelson margins.

Distribution. New Zealand: west coast of North and South islands. At depths of 1120–1313 m.

Natatolana imicola (Dollfus, 1903)

Synonymy in Keable & Bruce, 1997: 688, figs. 13–15.

Type material of *N. imicola*. Syntypes: all IOM; unknown number of specimens, Station 209; 7♂♂, 11♀♀, 36 0257, Station 228 (cited as 238); ♀, 36 0252, Station 553; 2♂♂ (mature), male (immature), 3♀♀, 36 0256, Station 846. All examined except those from station 209. • Type locality of *N. imicola*: Atlantique, 39°18.08'N 33°32.25'W, 1372 m, [*Campagnes de l'Hirondelle et de la Princesse Alice* Station 209]; Atlantique, 38°22.38'N 30°42.78'W, 1924 m, [*Campagnes de l'Hirondelle et de la Princesse Alice* Station 228 (cited as 238)]; Atlantique, 37°42.67'N 27°25.5'W, 1385 m, [*Campagnes de l'Hirondelle et de la Princesse Alice* Station 553]; Atlantique, 30°01.5'N 27°46'W, 1638 m, [*Campagnes de l'Hirondelle et de la Princesse Alice* Station 846].

Type material of *N. schmidti*. Syntypes: ovigerous ♀ 13.5 mm, male 11 mm, manca 7 mm, ZMUC CRU150, *Ingolf* stn 25; ♀, 12.5 mm, manca 4.75 mm, ZMUC CRU151, *Thor* stn 99. All examined. • Type locality of *N. schmidti*: Davis Strait, 63°30'N 54°25'W, 1064 m, [Danish *Ingolf* Expedition Station 25]; west of the most southern of the Färoe Islands, 61°15'N 9°35'W, 872–970 m, [*Thor* stn 99].

Material examined. Listed by Keable & Bruce (1997).

Diagnosis. *Eyes*: vestigial, or absent (there is a very slight indication of ommatidia, possibly these become less distinct with preservation). *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing posteriorly. *Antenna*: c. 0.37× as long as body, reaching to between approximately half way along pereonite 3 and posterior of pereonite 4. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.9× basal width; anterodorsal depression absent (although there is a slight depression it is not equivalent to the distinct and abrupt depression found in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 8–12 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: ischium anterodistal angle produced, but not as produced as on pereopods 1 and 2, similar to pereopod 4. Propodus with 2 RS on palm. *Pereopod 7*: basis narrow, width 0.4× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; margins very strongly curved laterally; broad; apex not at angle to adjacent margins, club shaped with a lateral notch. *Uropods*: exopod slightly shorter than endopod, 0.82× the length of the endopod.

Variation. The development of penes and the appendix masculina varies in male specimens, with the appendix masculina relatively straight and the vasa deferentia opening flush to the surface of the sternite. This variation does not appear to be correlated with size of the individual although it probably represents changes associated with maturity (Keable & Bruce, 1997).

Size. Smallest manca 4.75 mm and largest specimen (ovigerous female) 13.5 mm.

Remarks. *Natatolana imicola* was originally described as a subspecies of *N. neglecta*, Keable & Bruce (1997) redescribed it, elevated it to species rank and synonymized *N. schmidti* with it.

Characters that distinguish *N. imicola* from similar species are noted in the remarks for *N. rekohu*.

Distribution. northeastern Atlantic, Davis Strait and Färoe Islands, south to 30°N, westwards to 54°W. At depths of 872–2450 m.

Natatolana insignis Hobbins & Jones, 1993

Natatolana insignis Hobbins & Jones, 1993: 124, figs. 7–10.–Brusca *et al.*, 1995: 80.–Kensley, 2001: 230.

Cirolana albicaudata.–Barnard, 1936: 152, fig. 2a–c [misidentification, not *Natatolana albicaudata* (Stebbing, 1900)].

Type material. Holotype: ♂, SIF 19041. Paratypes: ♀, SIF 19042; 7♀♀ SIF 19043. None examined. • Type locality: Central Red Sea, 21°28.97'N 38°15.55'E, 740–785 m, [R. V. VALDIVIA, Station Va22-111 ST-235, 12 April 1979].

Material examined. **India**: 18, ZMUC CRU105, off Tranquebar, 11°6'N 80°5'E, coarse sand and mud, 148 m, Galathea stn 288, 21 Apr. 1951. **Thailand**: ♂, PMBC, Phuket Bay, c. 7°52'N 98°22'E, 10 Jul. 1981.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*:

lateral margins medially constricted. *Antenna*: c. 0.42× as long as body, reaching to approximately half way along pereonite 4. Flagellum digitate processes present in males. *Coxal plates*: furrows moderately developed, on all coxae (although only shown on coxae 4–7 in original description). *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.79× basal width; anterodorsal depression absent (although a depression is apparent it is not equivalent to the distinct and abrupt depression found in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins broadly rounded; lateral margins converging smoothly to a point; with 6–8 RS (8 in description but only 6 figured, 8 in material examined). *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 1 RS on palm. *Pereopod 7*: basis broad, width 0.54× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal three-quarters. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.75× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.63–0.75× the length of the endopod.

Sexual dimorphism. Females lack the digitate processes on the articles of the antennal flagellum.

Size. Adults to c. 10 mm.

Remarks. The presence of digitate processes on the articles of the antennal flagella in males of *Natatolana insignis* distinguish this species from all others in the genus. The shape of the uropod endopod is also highly distinctive, with a broadly rounded medial margin and distinct notch on the lateral margin.

Distribution and ecology. Red Sea; Arabian Sea; Gulf of Oman; India: Bombay and Tranquebar; Thailand: Phuket. At depths of 148–1825 m. Scavenger.

Natatolana intermedia (Vanhöffen, 1914)

Cirolana intermedia Vanhöffen, 1914: 500, fig. 37.–Tattersall, 1921: 205.–Hale, 1937: 17.–1952: 27.–Kussakin, 1967: 224.
Natatolana intermedia.–Bruce, 1981: 958.–1986: 222.–Brandt, 1988: 113, figs. 51–55.–Brusca *et al.*, 1995: 80.

Type material. Lectotype designated by Brandt (1988): ♂, 15.5 mm, originally ZMG but now in SIF ZMG 260 (not examined). Paralectotypes: ♂, 17 mm, 4♀♀, 13 mm, 14 mm, 15 mm, 16 mm, SIF ZMG 261 (not examined). Also, 2♂♂, ZMUC CRU158; 2♀♀, ZMUC CRU159; apparently part of original syntype series from the type locality donated by the ZMB in 1926 (examined). Other possible paralectotypes are ZMB 17618 (male and 2♀♀) ZMB 17620 (male and 6♀♀); all from type locality (Brandt, 1988) (not examined). • Type locality: off Gauss Station, Posadowsky Bay, Antarctica, 66°2.9'S 89°38.5'E, 385 m, [Deutsche Sudpolarexpedition 1901–1903].

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.33–0.4× as long as body, reaching to between the posterior of pereonite 3 and 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.92× basal width; anterodorsal depression absent (there is an indistinct depression but this is not as distinct and abrupt as in species such as *N. pellucida*); anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 10–16 RS. *Pereopod 2*: propodus with 3–4 RS on palm. *Pereopod 3*: propodus with 3–6 RS on palm. *Pereopod 7*: basis narrow, width 0.45× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; margins very strongly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.81× the length of the endopod.

Size. Females to 23 mm, males to 24 mm.

Remarks. *Natatolana intermedia* is most similar to *N. nitida* but has a rounded anteroventral corner on coxa 2, a pleotelson with convex posterolateral margins and a slender and strongly curved appendix masculina. *Natatolana obtusata* is also similar but has pleonite 4 with a sinuate posterodorsal margin.

Distribution. Antarctica: Gauss Station; McMurdo Sound; Banzare Coast; Kemp Coast; Davis Sea; Enderby Land; Lars Christensen Coast; Antarctic Peninsula; Weddell Sea (Brandt, 1988). At depths of 163–560 m (Kussakin, 1967).

Natatolana japonensis (Richardson, 1904)

Synonymy in Keable, 1996a: 8, figs. 1–3. Additional listings and records of this species are those of Nierstrasz (1931, p. 158), Brusca *et al.* (1995, p. 80), Saito *et al.* (2000, p. 64), Yu & Li (2001, p. 263), Nunomura (2004, p. 356).

Type material of *N. japonensis*. Holotype: ♂, 18 mm, USNM 29085 (examined). • Type locality of *N. japonensis*: Yokkaichi Light, Japan, [c. 35°02'N 136°40'E].

Type material of *N. miyamotoi*. Holotype: ♂, TSM TOYA Cr-10793 (not examined). Allotype: ♀, TSM TOYA Cr-10794 (not examined). Paratypes: 2, TSM TOYA Cr-10795-10796 (examined). • Type locality of *N. miyamotoi*: Off Iwase, Toyama City, Japan [36°43.6'N 137°14.7'E], 20 m.

Material examined. Listed by Keable (1996a).

Diagnosis. *Interocular furrow*: well developed, forming a ridge that extends across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.3–0.46× as long as body, reaching to between the posterior of pereonite 3 and 4. *Coxal plates*: furrows variously developed, complete but faint on coxae 2–5 and 7, very faint and incomplete or absent on coxa 6. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.81–0.85× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle or convex; apex not produced, lateral margins converging smoothly to a point; with 10–12 RS. *Pereopod 2*: propodus with 1 RS on palm. *Pereopod 3*: ischium anterodistal angle produced, but not as produced as on pereopods 1 and 2, similar to pereopod 4. Propodus with 1 RS on palm (and apparently a socket for another 1). *Pereopod 7*: basis of medium breadth, or broad, width 0.5–0.56× length; distance between anterior margin and medial

carina less than between posterior margin and medial carina; posterior margin with setae on proximal quarter. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.04× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.93× the length of the endopod.

Variation. The posterior of the pleotelson appears to become broader as individuals increase in size. Of the material examined one specimen from off Iwase (TSM Cr 10796), 14 mm long, has the posterior margins of the pleotelson less distinctly angled to the anterolateral margins and has a more acute apex than in the holotype of *N. japonensis*. Another specimen from the same locality (TSM Cr 10795) is, however, 23 mm long and has a pleotelson identical in shape to that of *N. japonensis*. The holotype (USNM 29085) is the only specimen examined that has 10 robust setae on the pleotelson, other specimens have either 11 or 12.

Size. Adult specimens examined range from 12 mm to 26 mm.

Remarks. *Natatolana japonensis* was redescribed by Keable (1996). It can most readily be distinguished from other species of *Natatolana* by the following characters: size and shape of the eyes, length of the antenna, shape of the lateral margins of pleonite 4, shape, size and setation of the pleotelson and uropods and absence of penes.

Distribution. Japan, Korea and China. At depths of 6–439 m (Iwasa, 1965; Nunomura, 2004).

Natatolana kahiba Bruce, 1986

Natatolana kahiba Bruce, 1986: 111, fig. 76.–Springthorpe & Lowry, 1994: 48.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 150.

Type material. Holotype: ♀, 8.2 mm, ZMUC CRU1693. Paratype: AM P32175. All examined. • Type locality: 5 km south of North Solitary Island [originally cited as off Cape Byron, corrected by Springthorpe & Lowry (1994)], NSW, Australia, 29°57'S 153°24'E, 75 m.

Material examined. **New South Wales**: 37, AM P47283, east of Coffs Harbour, 30°17.49'S 153°13.90'E, 45.4 m, 11–12 Aug. 1993, SEAS NSW-873; 7, AM P47284, off Rosherville Beach, Port Jackson, 33°48.9'S 151°15.0'E, baited trap, 10 m, S. Keable & J. Lowry, 8–9 May 1988, stn 10. **Tasmania**: many, AM P47285, mouth of Fortescue Bay, 43°07.77'S 145°59.47'E, baited trap, 50 m, 17–18 April 1993, SEAS TAS-368.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.2–0.25× as long as body, reaching to between the posterior of pereonites 1–2 (holotype pereonite 1, paratype pereonite 2). *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.9× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 4 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.66× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.94× length of endopod; margins straight or very slightly curved laterally; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod short, 0.71× the length of the endopod.

Variation. The antennal flagellum of the holotype and paratype has 12 and 15 articles, respectively. In material examined from Coffs Harbour (AM P47283) near the type locality and in Port Jackson (AM P47284) there are up to 18 articles in the antennal flagellum.

Size. Adults to c. 25 mm.

Remarks. This is the first record of a male specimen of *Natatolana kahiba*. This species is most similar to *N. bulba*, *N. arrama* and *N. woodjonesi*. It can be most easily separated from these species by the presence of two to three robust setae on the lateral margin of the uropod exopod.

Bruce (1986, p. 111) described small spines (= robust setae) on the palm of the propodus of pereopods 2 and 3 of this species. Absence of these robust setae is, however, regarded by Bruce (1986) as a diagnostic character of species in the *Natatolana woodjonesi* group, into which he places *N. kahiba*, and in his key to species *N. kahiba* can only be reached if it is assumed that these robust setae are absent. Examination of these setae in *N. kahiba* indicates they are minute and easily overlooked. They do not appear to be homologous to the robust setae found in this position in other species because in *N. kahiba* they are slender and flexible and appear to have their base on the lateral margin of the pereopod rather than the palm itself. This observation is consistent with the placement of *N. kahiba* in the *N. woodjonesi* group and key to species by Bruce (1986).

Distribution and ecology. Australia: northern and central New South Wales; Tasmania. At depths of 10–75 m. Scavenger.

Natatolana karkarook Bruce, 1986

Natatolana karkarook Bruce, 1986: 69, figs. 44, 45.–Springthorpe & Lowry, 1994: 49.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 151.

Type material. Holotype: ♀, 20.8 mm, AM P30335. Paratype: ♀, AM P30336. All examined. • Type locality: Cairns Reef, Cooktown, Queensland, Australia, 15°42'S 145°33'E.

Material examined. Northern Territory: ♂, NTM Cr009861, Gove, 12°12'S 136°43'E, 0 m, R. Hanley *et al.*, 20 Nov. 1991, RH91-115. **Queensland**: manca, QM W18886, Gulf of Carpentaria, 15°57'S 138°41.8'E, grab, 25 m, CSIRO, 11 Dec. 1990.

Diagnosis. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Labrum*: with acute laminar projection. *Antenna*: c. 0.16–0.22× as long as body, reaching to between the posterior of pereonite 1 and the posterior of pereonite 2. *Coxal plates*: furrows variously developed, incomplete and on coxae 2–3 only. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.76× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle or convex; apex not produced, lateral margins converging smoothly to a point; with 8–12 RS. *Pereopod 2*: propodus with 1 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.55× length; distance between anterior

margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal half. *Penes*: absent, vasa deferentia opening flush to surface of sternite 7 (area around openings slightly raised but not forming flexible processes). *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.94× length of endopod; slender; margins bent slightly medially; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.85× the length of the endopod.

Variation. The holotype has 12 robust setae on the pleotelson margin, the paratype has nine and the male from Gove (NTM Cr009861) has eight.

Size. Adults to 20.8 mm.

Remarks. This is the first record of a male specimen of *Natatolana karkarook*. This species is unique in having an acute laminar projection on the labrum, the shape of the pleotelson coupled with the relatively short antennae are also distinctive and the mouthparts are unusual (as discussed in remarks for *N. buzwilsoni*).

Distribution. Australia: Gove, Northern Territory; Gulf of Carpentaria; Cooktown, Queensland. Intertidal to 25 m depth.

Natatolana laewilla Bruce, 1986

Natatolana laewilla Bruce, 1986: 85, figs. 56, 57.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 151.
Natatolana leawilla.–Springthorpe & Lowry, 1994: 51 [*lapsus*].

Type material. Holotype: ♀, AM P33551. Paratypes: AM P33550, P33552. All examined. • Type locality: east of Port Jackson, NSW, Australia, 33°36'S 152°05'E, 1090–1125 m.

Material examined. **Queensland**: series from off Flynn Reef, 16°37.81'S 146°23.08'E, 1000m, 6–8 Jun. 1993: 1, AM P47300, SEAS QLD-932; 6, AM P47301, SEAS QLD-950. **New South Wales**: series from northeast of Coffs Harbour, 1000m, 11–13 Aug. 1993; 15, AM P47302, 30°10.88'S 153°32.21'E, SEAS NSW-877; 7, AM P47303, 30°10.94'S 153°32.27'E, SEAS NSW-862. **Tasmania**: 8, AM P47304, east of Fortescue Bay, 43°08.96'S 145°15.36'E, 1000 m, 8–9 April 1994, SEAS TAS-403.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins sinuate. *Antenna*: c. 0.35× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed or completely absent on all coxae, if present may be weakly developed on all or only some coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.81× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 10 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopod 2*: propodus with 0–1 RS on palm (the holotype has one robust seta on one side, in the other material examined these setae may be present or absent). *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.46× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; slender; margins strongly or very strongly curved laterally; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.82× the length of the endopod.

Variation. Indistinct to well-developed coxal furrows are apparent on all coxae in some type material and the material examined from Queensland. The holotype and some material examined from Queensland has a robust seta on the propodal palm of pereopod 2. Conspicuously elongated robust setae were only present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males from Queensland. None of the male specimens in the non-type material examined had the appendix masculina as strongly curved as in the type material.

Sexual dimorphism. Females lack the conspicuously elongated robust setae that may be present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. In type material females to 9.5 mm, males to 7.5 mm. Non-type material to c. 15 mm.

Remarks. *Natatolana laewilla* can be separated from all other species in the genus by the reduced eyes and the presence of a distinct dorsal depression on the pleotelson.

Distribution and ecology. Australia: Cairns, Queensland to Tasmania. At depths of 880–1125 m. Scavenger.

Natatolana lilliput n.sp.

Figs. 31–32

Type material. HOLOTYPE: ♂, 12 mm, AM P47237. PARATYPE: ♂, TM. • Type locality: about 0.5 km east of shore, Garretts Bight, Tasmania, Australia, 43°22.2'S 147°3.6'E, [baited trap], 25 m, [J.K. Lowry & S.J. Keable, 20–21 April 1991, TAS-228].

Additional material. **Tasmania**: 32, AM P47238, about 50 m off south side of Huon Point, 43°17.6'S 147°5.9'E, baited trap, probably sandy bottom, 13 m, J.K. Lowry & S.J. Keable, 18–19 April 1991, TAS-188; 7, AM P47239, in the middle of the cove on the south side of Huon Point, 43°17.8'S 147°5.2'E, baited trap, probably muddy substrate, 18 m, J.K. Lowry & S.J. Keable, 18–19 April 1991, TAS-191; 1, AM P47240, in small cove just north of Esperance Point, 43°19.5'S 147°4.1'E, baited trap, probably rocky substrate, 3 m, J.K. Lowry & S.J. Keable, 18–19 April 1991, TAS-196.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.17× as long as body, reaching to approximately one third of the way along pereonite 2. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.89× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 4–6 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.71× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal two-thirds. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.94× length of endopod; margins bent slightly medially; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.76× the length of the endopod.

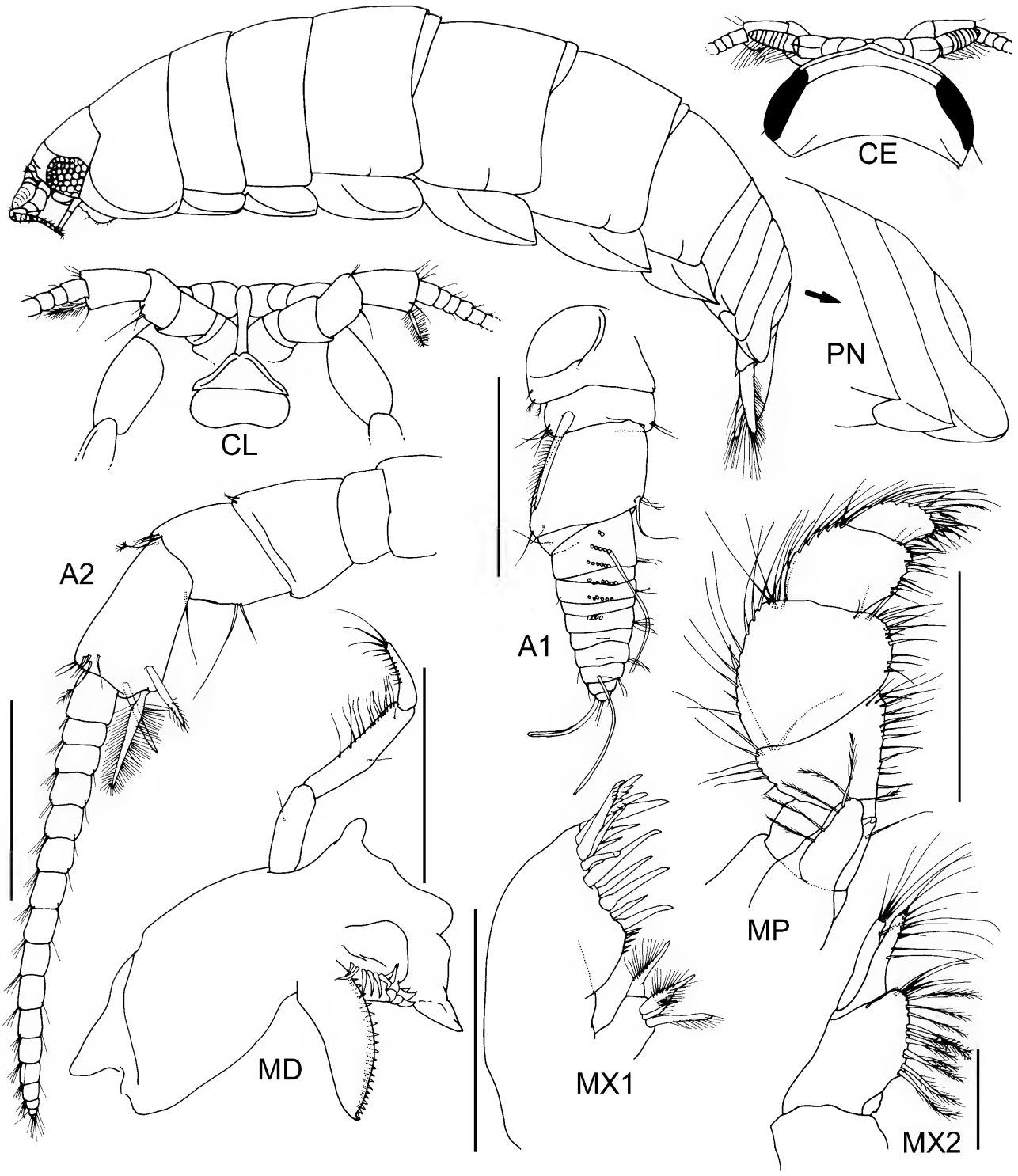

Fig. 31. *Natatolana lilliput* n.sp., holotype. Scales = 0.5 mm, except MX2 = 0.2 mm.

Additional descriptive characters. Based on holotype. *Body*: length c. 4× width. Colour cream/tan in alcohol. Chromatophores absent. *Eyes*: with 8 ommatidia in horizontal diameter; with 7 ommatidia in vertical diameter; round with upper margin flat; colour tan in alcohol. *Frontal lamina*: length c. 5× basal width; apex expanded, anterior margin rounded. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 2 SS medially on posterolateral margin, 1 SS at posterodistal angle, 4 SS and 1 penicillate seta at anterodistal angle; article 5 with 2 conspicuous pappose setae and 1 SS at posterodistal angle, 5 SS and 1 penicillate seta at anterodistal angle. Flagellum 17-articulate. *Mandible*: setal row with 13 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae (left side) or with 3 large robust pappose setae (right side); lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 5 SS; medial lobe with 6 SS and 10 PS; middle lobe with 10 SS.

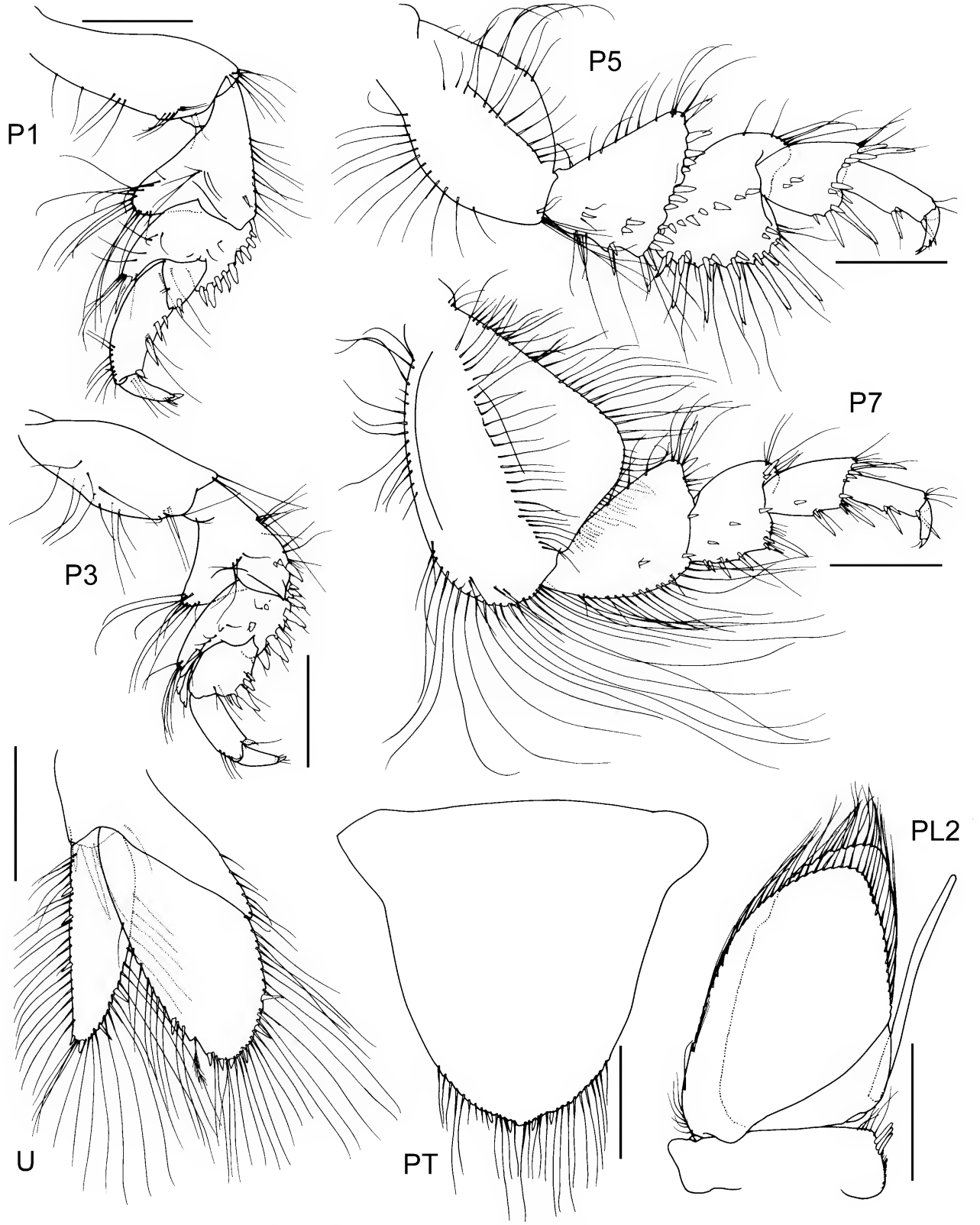

Fig. 32. *Natatolana lilliput* n.sp., holotype. Scales = 0.5 mm.

Maxilliped: endite with 1 coupling hook, and 6 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–7; pereonites 4–6 subequal and longer than 1 and 7 which are subequal and longer than 2–3. *Coxae*: pereonite 1, coxae 2–4 with rounded posteroventral corners, coxae 5–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex, PS present. Ischium anterior margin

with SS; posterior margin without RS (1 submarginally), PS present. Merus posterior margin with 6 RS, SS present. Carpus posterior margin with 2 RS (and 1 submarginally), 1 SS. Propodus subequal to carpus; posterior margin with 3 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 3 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 2 RS and 1 penicillate seta, PS on distal two-thirds. Exopod medial margin convex, with 2 RS, PS on distal three-quarters; apex acute, with 2 RS; lateral margin straight, with 3 RS, PS along entire length.

Variation. The holotype has four robust setae on the pleotelson. Of 42 additional specimens examined five (12%) have a damaged pleotelson, two (5%) have six robust setae on the pleotelson, eight (19%) have five robust setae on the pleotelson and 27 (64%) have four. Some of the specimens from Huon Point (AM P47239) have orange pigment on the posterolateral margins of pleonite 4 and on the uropod peduncle.

Size. Adults to 14 mm.

Etymology. Derived from Lilliput, a place in the novel Gulliver's Travels by Jonathan Swift where everything is reduced in size, in reference to the short nature of the antennae.

Remarks. *Natatolana lilliput* can be most readily separated from similar species by the following characters: the short antennae that reach just beyond the posterior margin of pereonite 1 and have relatively few flagellar articles; the complete interocular furrow; the rounded apices and posterior margins of the uropod endopod and pleotelson. *Natatolana kahiba* is most similar but has an incomplete interocular furrow. *Natatolana rusteni* n.sp. is also similar but differs in having a narrow and more acute pleotelson, usually with six robust setae on the posterolateral margins, an incomplete interocular furrow and slightly shorter antennae with fewer articles in the flagella.

Distribution and ecology. Australia: known only from the east coast of Tasmania. At depths of 3–25 m. Scavenger.

Natatolana longispina Bruce, 1986

Natatolana longispina Bruce, 1986: 82, figs. 54, 55.–Springthorpe & Lowry, 1994: 51.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 151.

Cirolana corpulenta.–Hale, 1940: 289 (part) [mis-identification, not *Natatolana corpulenta* (Hale, 1925)].

Natatolana corpulenta.–Bruce, 1986: 79, figs. 51–53 (part) [mis-identification, not *Natatolana corpulenta* (Hale, 1925)].

Type material. Holotype: ♂, 8.8 mm, NMV J1770 (not examined). Paratypes: NMV J1771–1783 (not examined); AM P32371–32374 (examined); USNM (not examined). • Type locality: Western Port, Victoria, Australia, 38°27'S 145°14'E.

Material examined. **New South Wales**: series from 1.5 km east of Belmont Beach, near Newcastle, 33°02.36'S 151°41'E, shipek [grab], AM Hunter District Water Board Survey (reported by Bruce [1986]); 1, AM P23035, 23 m, 16 Dec. 1975; manca, AM P23042, 20 Sep. 1975; 1, AM P23047, 22 m, 10 Jun. 1975; ♀, AM P47153, between Merimbula Point and Haystack Rock, Merimbula, 36°56.4'S 149°56.9'E, baited trap, sand, J. Lowry & S. Keable, 1–2 Dec. 1988, NSW-406; 3, AM P47154, off Wattamolla, 34°44'S 150°39'E, baited trap, unknown substrate, 40 m, J. Lowry, 13–14 Nov. 1990, NSW-431; 220, AM P47157, off Providential Head, 34°44'S 150°39'E, baited trap, 25–30 m, S. Keable, A. Parker & J. Lowry, 14–15 Jan. 1991, PIO-103. **Victoria**: paratype ♀, AM P32372, Crib Point, Western Port, 38°22'S 145°12'E, 8m, Victorian Fisheries and Wildlife Department, 14 Jul. 1964, sample A1/2 no. 53588; 7 paratypes, AM P32373, Crib Point, Western Port, 38°22'S 145°12'E, sand, 11m, Victorian Fisheries and Wildlife Department 10 Mar. 1965, CPBS no. 53611. **Bass Strait**: ♂, ♀, NMV J1107, 39°02'S 143°14'E, grab, medium carbonate sand, 79 m, G. Poore, 8 Oct. 1980; 15, J1329, fine sand, 95 m, G. Gomon *et al.*, 31 Jan. 1981. **Tasmania**: ♀, AM E6757, Elliott Cove, west coast, [presumably 42°59'S 145°33'E], 9 m, FIS *Endeavour* Expedition 1909–14 (reported by Hale [1940]); series from baited traps, J. Lowry and S. Keable: 3, AM P47139, due north of Lomas Point, Port Esperance, 43°20.8'S 147°3.3'E, probably sandy bottom, 10 m, 19–20 April 1991, TAS-201; D'Entrecasteaux Channel: 47, AM P47140, 43°22.2°S 147°3.2'E, 13 m, 20–21 April 1991, TAS-226; 20, AM P47147, 43°22.2 147°3.4'E, 21 m, 20–21 April 1991, TAS-227; 23, AM P47142, 43°22.2 147°3.6'E, 25 m, 20–21 April 1991, TAS-228; Bruny Island: 9, AM P47143, 43°21.5'S 147°22.2'E, sandy bottom, 25 m, 24–25 April 1991, TAS-267; 3, AM P47144, 43°21.5'S 147°22.3'E, sandy bottom, 28 m, 24–25 April 1991, TAS-268; 1, AM P47145, 43°21.3'S 147°22.4'E, sandy bottom, 28 m, 24–25 April 1991, TAS-269; 12, AM P47146, 43°21.5'S 147°22.2'E, sandy bottom, 24 m, 24–25 April 1991, TAS-271; 2, AM P47147, 43°21.1'S 147°22.4'E, sandy bottom, 28 m, 24–25 April 1991, TAS-272; Cape Sorell: 6, AM P47148, 42°11.5'S 145°11'E, sand and detritus, 18 m, 26–27 April 1991, TAS-277; 10, AM P47149, 42°11.5'S 145°11'E, sand and detritus, 25 m, 26–27 April 1991, TAS-278; ♂, AM P47150, 42°11.5'S 145°11.4'E, sand, 25 m, 26–27 April 1991, TAS-282; 2, AM P47151, 42°09.4'S 145°15'E, sandy bottom, 16 m, 27–28 April 1991, TAS-304; Freycinet Peninsula: 146, AM P47152, 42°17'S 148°18.8'E, 45 m, 30 April–1 May 1991, TAS-337.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.35× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows strongly developed, on coxae 2–7. Pereonite 1, coxa 2 posterior margins sinuate, posteroventral corners developed into weak coxal points. Pleonite 4: apex forming a broad acute point. *Pleotelson*: broad, length 0.73× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 10 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.47× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; slender; margins sinuate; apex recurved, bent slightly medially, acute. *Uropods*: exopod slightly shorter than endopod.

Variation. In the material examined, there is a slight variation in the production of the pleotelson apex. The specimens from near Cape Sorell (AM P47148–47151) have the apex more produced than the other specimens identified as *Natatolana longispina*.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Females to 12.7 mm, males to 8.8 mm, mancas to 5.6 mm.

Remarks. Bruce (1986) noted that *Natatolana longispina* is similar to *N. corpulenta*. These two species can be easily separated by the anteroventral corner of coxa 2, it is rounded in *N. longispina* and produced into an acute tooth in *N. corpulenta*.

Distribution. Australia: southern and central New South Wales; Port Phillip Bay and Western Port, Victoria; Bass Strait; east and west coasts of Tasmania. At depths of 9–95 m.

Natatolana lowryi Keable, 1997

Natatolana lowryi Keable, 1997: 256, figs. 2–4.–Bruce *et al.*, 2002: 151.

Type material. Holotype: ♂, 15.3 mm, NTM Cr-011523. Paratypes: ♀, manca, AM P44852; ♂, NTM Cr-011508; ♂, ZMUC CRU1713; ♂, USNM 264079. All examined. • Type locality: Middle Arm, west of Channel Island, Darwin Harbour, NT, Australia, 12°33.7'S 130°50.7'E, [baited trap, unknown substrate, probably muddy sediment], 2 m, [S. Keable, 12–13 Jul. 1993, NT-148].

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.2× as long as body, reaching to posterior of pereonite 1. *Coxal plates*: furrows variously developed, incomplete furrows on coxae 3 and 4, absent on other coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: narrow, length 1.01× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, contiguous with anterolateral margins; apex not produced, lateral margins converging smoothly to a point; with 10–14 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth, width 0.46× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal quarter. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.09× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, acute. *Uropods*: exopod short, 0.77× the length of the endopod.

Variation. The holotype specimen has 11 robust setae on the pleotelson margin, the majority of other specimens in the type series have 12 robust setae on the pleotelson and the other material reported by Keable (1997) mostly has 14 robust setae on the pleotelson.

Size. Adults to c. 20 mm.

Remarks. *Natatolana lowryi* is most similar to *N. luticola*. It is separated from that species by the posterolateral margins of the pleotelson being less markedly angled to the anterolateral margins and by having a more acute angle at the apex of the pleotelson. The fringe of long slender setae on the posterior margin of the antennal peduncular article 4 is also a distinctive character state for this species.

Distribution and ecology. Australia: Darwin and Gove, Northern Territory; Gulf of Carpentaria. At depths of 2–55 m. Scavenger.

Natatolana luticola (Holdich, Harrison & Bruce, 1981)

Cirolana luticola Holdich *et al.*, 1981: 569, fig. 6 (part).
Natatolana luticola.–Bruce, 1981: 958.–1986: 101, fig. 69.–Brusca *et al.*, 1995: 80.–Keable, 1997: 261.–Bruce *et al.*, 2002: 151.

Type material. Holotype: ♂, 10.4 mm, QM W6339. Paratypes: ♀, QM W6340 (mis-identification = *Natatolana angula* Bruce, 1986 according to Bruce [1986]); lots of 1 manca, 1♂, 1♂, 1♀ and 7♂♂, 6♀♀ and 9 mancas, recorded by Holdich *et al.* (1981) but institution where deposited not stated, possibly in Nottingham University. According to Bruce (1986) the adult male paratype shown by Holdich *et al.* (1981) in figs. a–c,h,j,l is *N. angula* not *N. luticola*. None examined. • Type locality: Halifax Bay, Queensland, Australia [c. 19°05'S 146°40'E], 14.5 m.

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.21–0.3× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.75× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle; apex not produced, lateral margins converging smoothly to a point; with 12 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.53× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.76× the length of the endopod.

Size. Adults to 13.6 mm.

Remarks. The angular pleotelson with a relatively high number of robust setae, well-developed rounded eye, incomplete interocular furrow and relatively narrow basis on pereopod 7 are sufficient characters to distinguish *Natatolana luticola* from all other species in the genus.

Distribution and ecology. Australia: Darwin Harbour and Gove, Northern Territory; northern Queensland south to Halifax Bay. At depths of 1.9–49 m. Scavenger.

Natatolana matong Bruce, 1986

Natatolana matong Bruce, 1986: 93, figs. 62, 63.–Springthorpe & Lowry, 1994: 52.–Brusca *et al.*, 1995: 80.–Bruce *et al.*, 2002: 151.
Cirolana rossi.–Hale, 1952: 24 [mis-identification, not *Natatolana rossi* (Miers, 1876)].

Type material. Holotype: ♂, TM G2543 (not examined). Paratypes: TM G2193; NMV J920, J1733; SAMA C3277, C3921; USNM 109986; BMNH (not examined); AM P33546 (examined). • Type locality: off King Island, northwest Tasmania, Australia, c. 40°00'S 144°00'E.

Material examined. **New South Wales**: series from off Wollongong: 6, AM P46924, 34°32.02'S 151°13.00'E, 200 m, 6–7 May 1993, SEAS NSW-780; 5, AM P44415, 34°33.01'S

151°16.54'E, 400 m, 7–8 May 1993, SEAS NSW-803. **Tasmania**: 9, AM P47453, east of Fortescue Bay, 43°09.37'S 145°13.6'E, baited trap, 300 m, 16–17 April 1993, SEAS TAS-361.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon (the feeble trace of a furrow that curves anteriorly from the point of termination of the distinct furrow, described by Bruce (1986), appears in the paratype material to be equivalent to the complete interocular furrow of other taxa examined [e.g., *N. rossi*]); produced medially. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.33× as long as body, reaching to just beyond the posterior of pereonite 3. *Coxal plates*: furrows variously developed, coxae 2–3 with faint but complete furrows, coxa 4 with a faint partial furrow, coxae 5–6 without furrows and coxa 7 with a feeble trace of a furrow (on some specimens examined (AM P46924) nearly complete coxal furrows are present on all coxae). *Pleonite 4*: apex forming a narrow acute point. *Pleotelson*: broad, length 0.76× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute or obtuse angle (angle about 90°); apex not produced, lateral margins converging smoothly to a point; with 12 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 3 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; margins straight; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.9× the length of the endopod.

Size. Adults to c. 40 mm.

Remarks. *Natatolana matong* is extremely similar to *N. rossi*. The development of the interocular and coxal furrows does not reliably separate the two species as suggested by Bruce (1986). The shape of pleonite 4, however, is consistently different between the two species, *N. rossi* having a more sinuate posterodorsal margin. *Natatolana hirtipes* is also similar but has a smoothly convex interocular furrow (sinuate in *N. matong*), a broader basis of pereopod 7 and pleonite 4 with a more strongly sinuate posterodorsal margin.

Distribution and ecology. Australia: off Wollongong, New South Wales; off east and northwest Tasmania At depths of 155–400 m. Scavenger.

Natatolana meridionalis (Hodgson, 1910)

Cirolana meridionalis Hodgson, 1910: 20, pl. 3.–?Stephensen, 1947: 24, fig. 7.

Natatolana meridionalis.–Bruce 1981: 958.–1986: 218, 222.–Brandt 1988: 102.–Brusca *et al.*, 1995: 80.–Castelló, 1999: 278.–Takeuchi *et al.*, 2001: 624.

Cirolana albinota Vanhöffen, 1914: 497, fig. 35.–Monod, 1931: 22.–Hale, 1952: 26.–?Menzies 1962: 126, fig. 41, F–G.–Kussakin, 1967: 223.–Carvacho 1977: 40.

Natatolana albinota.–Bruce, 1981: 958.–1986: 218, 222.–Brandt, 1988: 105, figs. 45–50.

Type material of *N. meridionalis*. Holotype: ♀, 35 mm, BMNH 1910.3.18:39-40 (examined). • Type locality of *N. meridionalis*: Winter Quarters, National Antarctic Expedition 1901–1904, Antarctica, [78°S 165°E, fide Stephensen (1947), 29 Aug. 1903, trap], 25 fathoms. Hodgson (1910) mentions another mutilated specimen found in a seal's stomach. The description, however, appears to have been based entirely on the intact specimen taken in the trap. There are two specimens in the type lot, the larger female specimen is the holotype. The smaller female specimen appears to be the specimen from the seal's stomach. A note with the smaller specimen reads "The damaged specimen, with eyes, is probably *C. [Natatolana] intermedia*, Vanhöffen (note by W.M. Tattersall)"; this identification by Tattersall appears to be correct.

Type material of *N. albinota*. Lectotype designated by Brandt (1988): ♂, 40.5 mm, originally ZMG but now in SIF, ZMG 259. Paralectotypes: 3♂♂, 37 mm, 40 mm, 42 mm, 3♀♀, 35 mm, 35 mm (ovigerous), 43 mm (ovigerous), SIF, ZMG 258. None examined. Also, 2♂♂, ZMUC CRU153; 2♀♀, ZMUC CRU154; apparently part of original syntype series from the type locality donated by the ZMB in 1926 (examined). • Type locality of *N. albinota*: Gauss Station, Posadowsky Bay, Antarctica, 66°2.9'S 89°38.5'E, 385 m, [Deutsche Sudpolarexpedition 1901–1903].

Diagnosis. *Eyes*: well developed or vestigial (apparently fading with preservation). *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.33× as long as body, reaching to posterior of pereonite 3 or half way along pereonite 4. *Coxal plates*: furrows moderately developed or strongly developed, on all coxae. Pereonite 1, coxa 2 posterior margins straight or slightly convex, or sinuate. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.9× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 12–18 RS. *Pereopod 2*: propodus with 4 RS on palm. *Pereopod 3*: propodus with 5 RS on palm. *Pereopod 7*: basis narrow, width 0.44× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae proximally and distally but not medially, or completely absent. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.16–1.27× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.91× the length of the endopod.

Size. Males to 42 mm, females to 43 mm (Brandt, 1988).

Remarks. Bruce (1986, p. 222) regarded *Natatolana albinota* to be a junior synonym of *N. meridionalis*. This synonymy was overlooked by Brandt (1988) as noted by Brusca *et al.* (1995, p. 80). Comparison of type specimens, of the two nominal taxa, supports the synonymy of Bruce (1986). Brandt (1988) used the absence of well-developed eyes in *N. meridionalis* to separate it from other Antarctic species of *Natatolana*, including *N. albinota* which was described as having small, light red eyes. Although the eyes of the holotype of *N. meridionalis* were described as absent (Hodgson, 1910), they are actually present with indistinct ommatidia that lack pigment. In other characters *N. meridionalis* resembles *N. albinota*, the difference in the appearance of the eyes is probably due to initial and subsequent preservation of the material examined by Brandt (1988) because the type material of *N. albinota* examined in this study also has indistinct weakly pigmented eyes.

Brandt (1988) discussed the records by Schultz (1977) of *Natatolana oculata* from southern Argentina, intimating that they were of *N. meridionalis* (= *N. albinota*). His illustrations, however, showing the posterior margins of the pleotelson and a relatively short appendix masculina, with a tapered apex, indicate he may have been describing another species, possibly *N. pastorei*. Schultz (1977, 1978) indicated that the record of *N. meridionalis* by Menzies (1962) from Chile may be *N. oculata*. Both of these records require verification by examination of the specimens.

Distribution and ecology. Antarctica: Discovery Bay, Davis Sea (Vanhöffen, 1914); Enderby Land and Pzydz Bay (Hale, 1952; Takeuchi *et al.*, 2001); Banzare Coast; Lars Christensen Coast; Ross Sea (Monod, 1931); Antarctic Peninsula; Weddell Sea; Scotia Sea. At depths of 35–670 m (Brandt, 1988). The records of Menzies (1962) from southern Chile require verification. Scavenger.

Natatolana nammuldi Bruce, 1986

Natatolana nammuldi Bruce, 1986: 113, figs. 77, 78.–Springthorpe & Lowry, 1994: 53.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 152.

Natatolana wullunya Bruce, 1986: 120, fig. 83.–Springthorpe & Lowry, 1994: 66.–Brusca *et al.*, 1995: 82.

Type material of *Natatolana nammuldi*. Holotype: ♀, 20.2 mm, NMV J1718 (not examined). Paratypes: NMV J1719–1722, J1753 (not examined); AM P32363–32365 (examined); USNM 190722 (not examined). • Type locality of *Natatolana nammuldi*: Western Port, Victoria, Australia, 38°27'S 145°14'E.

Type material of *Natatolana wullunya*. Holotype: ♀, 11.3 mm, AM P30364 (examined). • Type locality of *Natatolana wullunya*: off Sydney, NSW, Australia, 33°58'S 151°29'E, 150 m.

Material examined. **New South Wales**: 7, AM P47287, east of Coffs Harbour, 30°17.49'S 153°13.90'E, 45.4 m, 11–12 Aug. 1993, SEAS NSW-873; 53, AM P47288, between Lookout Point and Seahorse Shoals, Twofold Bay, 37°5.6'S 149°56.6'E, baited trap, unknown substrate, probably sediment, 30 m, J. Lowry & S. Keable, 28–29 Nov. 1988, NSW-392. **Tasmania**: series from east of Fortescue Bay, 43°09.37'S 145°13.6'E, 300 m, 16–18 April 1993; 8, AM P47289, SEAS TAS-361; 28, AM P47290, SEAS TAS-361; 24, AM P47291, SEAS TAS-378.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.27–0.3× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad or narrow, length 0.90–1.00× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle or convex; apex not produced, lateral margins converging smoothly to a point or produced into a small point; with 6–8 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.58× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.99× length of endopod; margins very slightly curved laterally; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.87–0.9× the length of the endopod; lateral margin with or without RS (present in type material).

Variation. In all samples specimens with eight robust setae on the pleotelson were most abundant but specimens with six robust setae were also common. In a sample from eastern Tasmania (AM P47291) forty percent of the specimens have four robust setae on the uropod endopod medial margin and the remainder has five. Two specimens from this sample were found to have three robust setae on the lateral margin of the uropod endopod as in the type material of *N. nammuldi*, whereas all other specimens examined have only two. The specimens in another sample from the same locality in eastern Tasmania (AM P47290) lack robust setae on the uropod exopod lateral margin, however, these could not be otherwise distinguished from specimens in the same sample (AM P47289, eight specimens) that have two to four robust setae on this margin.

Size. Adults from c. 11.3 mm to c. 27 mm, largest manca 7 mm.

Remarks. Bruce (1986) discussed the differences between *Natatolana nammuldi* and *N. woodjonesi* and *N. wowine*. Differences between *N. nammuldi* and *N. wullunya*, however, were not discussed. Bruce (1986) separated *N. wullunya* from all other species principally by its narrow frontal lamina. He also discussed other differences between *N. wullunya*, *N. arrama* and *N. woodjonesi*, including the shape of the frontal lamina, clypeus, pereopod 7, and number of robust setae on the pleotelson and lateral margin of the uropod exopod. Both *N. nammuldi* and *N. wullunya* were originally reported only from female specimens and single localities. For *N. wullunya* only a single specimen was recorded.

Comparison of type material of *Natatolana nammuldi* and *N. wullunya* indicates that any difference in the shape of the frontal lamina is relatively minor. The only other differences that could be found between the two nominal taxa are that the type material of *N. nammuldi* has eight robust setae on the pleotelson (except AM P32365 which has seven [six in *N. wullunya*]); five robust setae on the uropod endopod medial margin (four in *N. wullunya*); three robust setae on the uropod endopod lateral margin (two in *N. wullunya*); and four robust setae on the uropod exopod lateral margin (three in *N. wullunya*). The lateral margin of the uropod endopod is also slightly sinuate in the types of *N. nammuldi* (convex in *N. wullunya*) but this appears to be related to the larger size of the specimens. In the other material examined here, variations between the two extremes were found within samples, although most material had only two robust setae on the uropod endopod lateral margin.

Therefore, *Natatolana nammuldi* and *N. wullunya* appear to be synonymous as reported in Bruce *et al.* (2002) based on the unpublished thesis of Keable (1996). *Natatolana nammuldi* is recognized as the objective senior synonym because it has page precedence, a more accessible type locality and more type specimens than *N. wullunya*. Further material from the type localities of *N. nammuldi* and *N.wullunya* would help to confirm that the variation noted here is intra-specific.

Distribution and ecology. Australia: off Coffs Harbour/off Sydney/in Twofold Bay, New South Wales; Western Port,

Victoria; off the east coast of Tasmania. At depths of 8.1–300 m (the holotype of *N. wullunya* was collected from 150 m and the type material of *N. nammuldi* from c. 8.1 m). Scavenger.

Natatolana narica (Bowman, 1971)

Cirolana narica Bowman, 1971: 107, figs. 1–22.
Natatolana narica.–Bruce, 1981: 958.–1986: 64, 222.–Brusca *et al.*, 1995: 82.

Type material. Holotype: ♂, 21.8 mm, ZMUA Is. 100.527. Paratypes: ♂, 21.9 mm, USNM 139048; ?♀, 17.3 mm, ZMUA Is. 100.528. None examined. • Type locality: Banks Peninsula, South Island, New Zealand [43°50'S 173°E], from vestibular diverticulum of *Cephalorhynchus hectori*.

Material examined. **New Zealand**: ♂, 3♀♀, QM W18895, [Tasman Bay], 41.18°S, 173.16°E, 0 m, isopod trap, ex New Zealand Oceanographic Institute, K225A; ♂, ♀, NMNZ Cr 4434, Otago Harbour, 20.3 m, 23 Feb. 1962, loc. 10520.

Diagnosis. *Eyes*: vestigial (ommatidia are indistinct and lack pigment). *Interocular furrow*: well developed, forming a ridge that extends across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.3–0.4× as long as body, reaching to three-quarters of the way along pereonite 4. *Coxal plates*: furrows variously developed, incomplete and indistinct on coxae 2–4, 7. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.75× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins broadly rounded; apex not produced, truncate with a small medial point; with 8–12 RS (material examined 8–10, types described as having about 12). *Pereopod 2*: propodus with 0–1 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.56× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.06× length of endopod; margins straight or very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod longer than endopod, 1.15× the length of the endopod.

Size. Adults to c. 21 mm.

Remarks. *Natatolana narica* and *N. paranarica* n.sp. are the only species of *Natatolana* in which the uropod exopod is distinctly longer than the endopod. *Natatolana paranarica* is almost identical to *N. narica* but differs in that the posterolateral margins of the pleotelson meet at an acute angle, rather than being broadly rounded; the uropod endopod medial margin is smoothly convex, not sinuate; the ventral margin of the posterior coxae is straight not sinuate; there are slender setae at the uropod endopod and exopod apices that are shorter than the length of these rami, rather than being as long as them.

Distribution and ecology. New Zealand. Intertidal to 20.3m depth. *Natatolana narica* has been collected from nasal tract of a dolphin, it is unlikely to be a parasite as entry probably occurred while the dolphin was dead or dying (Bowman, 1971) and the species is likely to be a scavenger.

Natatolana natalensis (Barnard, 1940)

Figs. 33–35

Cirolana natalensis Barnard, 1940: 393.–Roman, 1970: 167.–Kensley, 1978: 69, fig. 28D.
Natatolana natalensis.–Bruce 1981: 958.–1986: 222.–Brusca *et al.*, 1995: 82.–Kensley, 2001: 230.

Type material. Lectotype: designated here, ♂, 12 mm, SAM-A8183 (examined). Paralectotypes: ♀, 16 mm (examined) and 2 others (not examined) SAM A-8183; 3 specimens, BMNH 1937.11.10.68 (examined). • Type locality: Illovo, Natal, South Africa, [30°06'S 30°51'E].

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows moderately developed on all coxae, difficult to see on coxae 2–4 and becoming increasingly weak on coxae 5–7. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: narrow, length 1× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 12 RS. *Pereopod 2*: propodus with 4 RS on palm. *Pereopod 3*: propodus with 4 RS on palm. *Pereopod 7*: basis broad, width 0.53× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.2× length of endopod; margins sinuate; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.85× the length of the endopod.

Additional descriptive characters. Based on lectotype. *Body*: length c. 2.5× width. Colour cream to white in alcohol. Chromatophores present, or absent (these are not obvious and appear to have faded after preservation). *Eyes*: with 9 ommatidia in horizontal diameter; with 9 ommatidia in vertical diameter; round; colour red in alcohol. *Frontal lamina*: length c. 3.4× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta and several smaller penicillate and SS; article 3 short, subequal to article 1. Flagellum 14-articulate. *Antenna*: peduncular article 4 with a group of 8 long SS and 1 penicillate seta on posterolateral margin; article 5 with 2 conspicuous pappose setae on posterolateral margin. Flagellum 23-articulate. *Mandible*: setal row with 14 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae and 1 SS; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 6 SS; medial lobe with 3 SS and 15 PS; middle lobe with 14 long SS on outer row and 3 short SS on inner row. *Maxilliped*: endite with 1 coupling hook, 6 PS and 1 SS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margins of all pereonites, oblique on pereonites 1–3, short straight and medial on pereonites 4–7; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: pereonite 1, coxae 2–4 with rounded posteroventral corners, coxae 5–7 with sinuate posterior margins formed into moderately large coxal points. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin convex; medial carina with PS along entire length; posterior

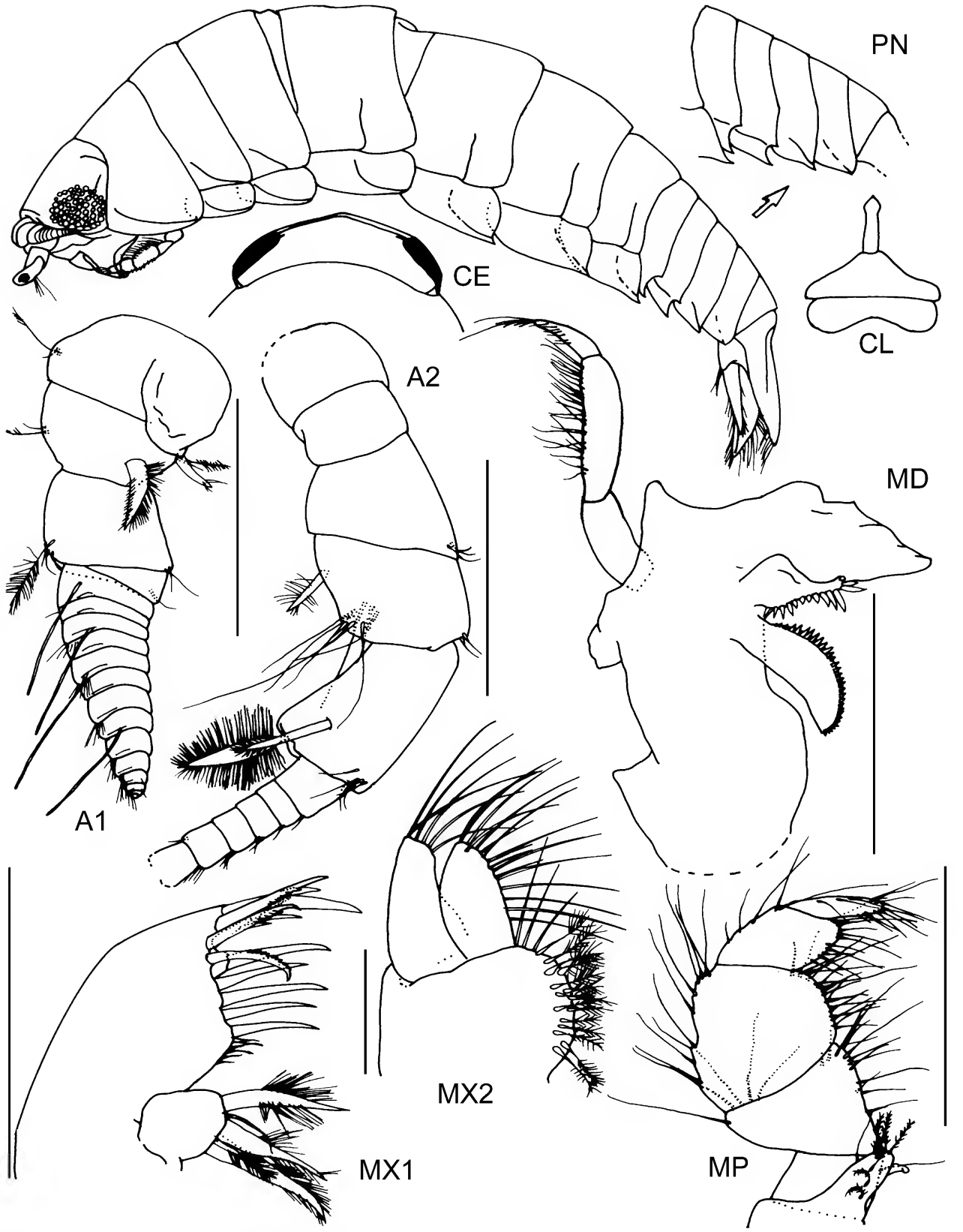

Fig. 33. *Natatolana natalensis*. Whole animal = paralectotype female, all other parts = lectotype male. Scales = 0.5 mm, except MX2 = 0.2 mm.

margin convex, SS present. Ischium anterior margin with SS; posterior margin with 3 RS (submarginal). Merus anterior margin with SS; posterior margin with 7 RS, SS present. Carpus posterior margin with 3 RS, SS present. Propodus subequal to carpus; posterior margin with 3 RS, SS present. *Pleopod 2 appendix masculina*: arising subbasally. *Pleopods 1–5*: exopod suture feebly developed on pleopods 3–5; endopod PS on most of margins of pleopods

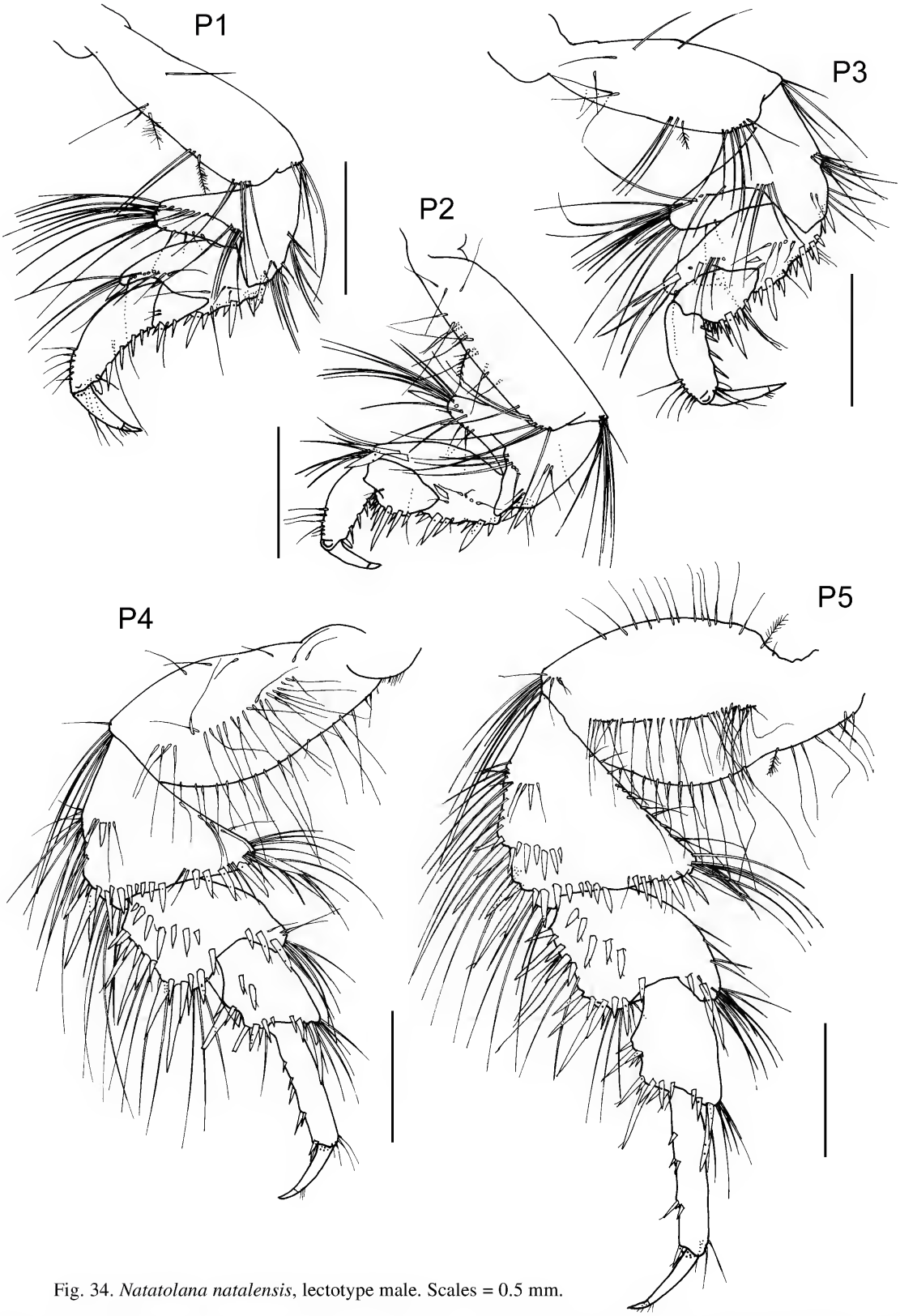

Fig. 34. *Natatolana natalensis*, lectotype male. Scales = 0.5 mm.

1–4, only 1 seta on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 3 RS, PS along entire length; apex with 2 RS; lateral margin angled close to midpoint, each half approximately straight, with 1 RS, PS along entire length. Exopod medial margin convex, with 2 RS, PS along entire length; apex acute, with 2 RS; lateral margin straight, with 5 RS, PS along entire length.

Size. Adults to 13 mm (Barnard, 1940; Kensley, 1978), but a female paralectotype in SAM A-8183 (newly measured) is 16 mm.

Remarks. It is unclear how many specimens were in the original type series of *Natatolana natalensis* but there were several and "no adult males or ovigerous females" (Barnard

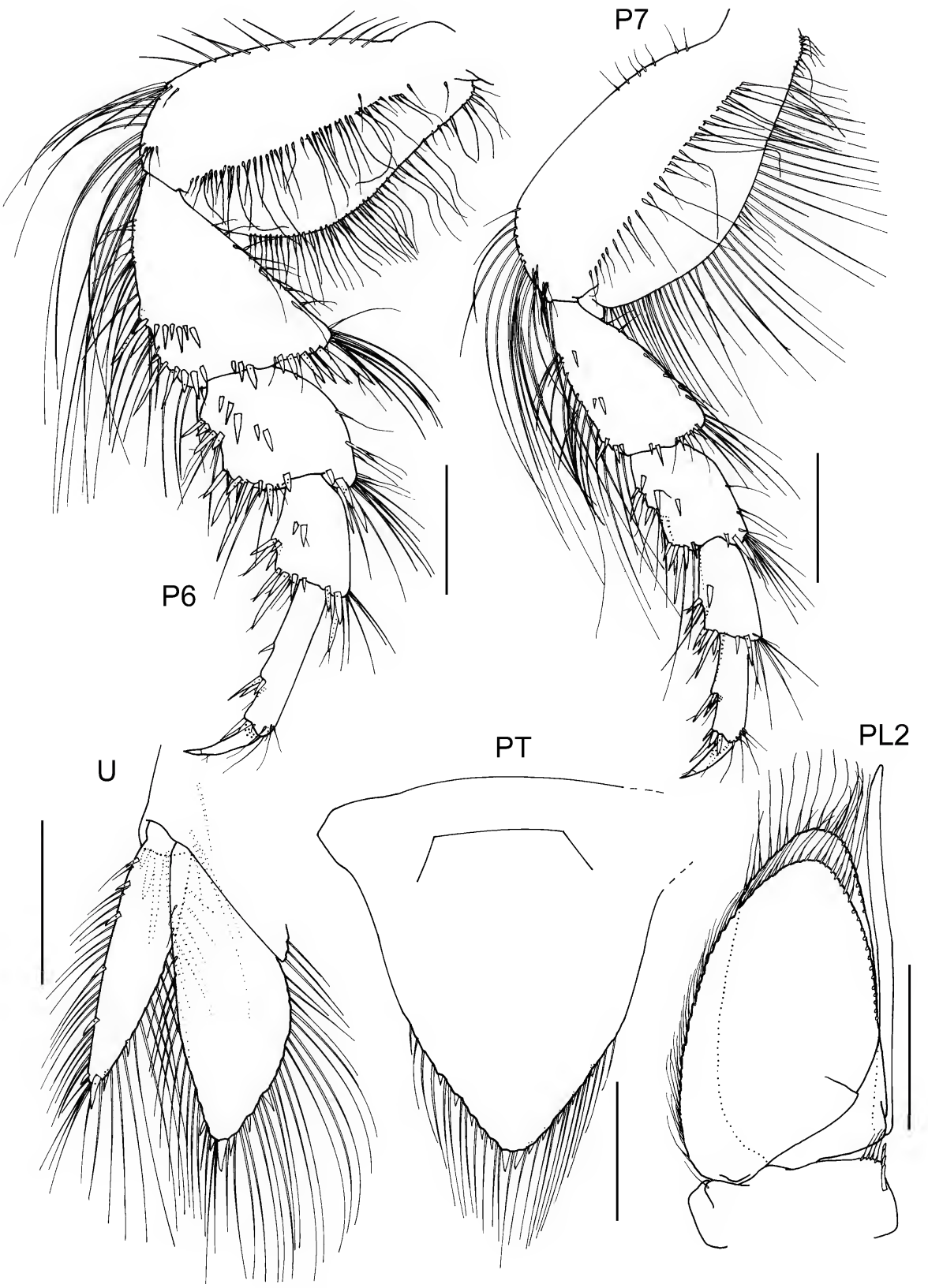

Fig. 35. *Natatolana natalensis*, lectotype male. Scales = 0.5 mm.

1940). Seven specimens were initially registered as types at the SAM but only four of these remain (L. Hoenson, SAM, *in litteris*), three apparently being transferred to the BMNH. The collection data on the label of the SAM type material (Illovo Beach, Natal. 1934. Det. Barnard) matches that given in the original description but contrary to the description the sample contains a well-developed male. Barnard did not illustrate the type material and the original description consists largely of a comparison to *N. hirtipes*, apparently based on the description of that species by

Hansen (1890). Because *N. natalensis* is difficult to identify from the original description, and from female specimens, the male is designated here as a lectotype to avoid future taxonomic confusion regarding identification of this species. The remaining type specimens become paralectotypes. The lectotype is consistent with Barnard's description and important characters, such as the 12 robust setae on the pleotelson, lack of an interocular furrow, rounded posterolateral margins of coxa 4 and shape of the pereopod 7 basis, match perfectly.

The distinct dorsal depression on the pleotelson, the presence of robust setae on the propodal palm of pereopods 2 and 3, the broad basis of pereopod 7 and the absence of penes in adult males, distinguish *N. natalensis* from all other species.

Distribution and ecology. South Africa: Natal. Madagascar. Shallow, infratidal-subtidal (Kensley, 1978; Bruce, 1986). Scavenger, "An enemy of fishes, and anglers' bête noire" (Barnard, 1940).

Natatolana natalis (Menzies & George, 1972)

Cirolana natalis Menzies & George, 1972: 24, figs. 14–15.
Natatolana natalis.–Bruce, 1981: 958.–1986: 222.–Brusca *et al.*, 1995: 82.

Type material. Holotype: ♂, 17 mm, USNM 121737 (examined). • Type locality: off Peru, Peru-Chile Trench, 08°23'S 80°25'W, 2966–2945 m, [ANTON BRUUN Sta. 161].

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.39× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad (original description states that the pleotelson is longer than wide but this does not appear to be measured using the basal width), length 0.89× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; RS present (these setae appear to have been rubbed off this margin but there seem to be sockets indicating the presence of at least 10). *Pereopod 2*: propodus with 6 RS on palm. *Pereopod 3*: propodus with 4 RS on palm. *Pereopod 7*: basis narrow, width 0.48× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae on distal half. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1× length of endopod; margins very strongly curved laterally; broad; apex not at angle to adjacent margins, with lateral projection forming a Y shape with acute apex. *Uropods*: exopod slightly shorter than endopod, 0.86× the length of the endopod; lateral margin RS unknown (originally illustrated as absent, uropod exopods are now missing from the holotype).

Size. Adults to 17 mm.

Remarks. The holotype is the only specimen recorded of *Natatolana natalis*. The original illustrations and description differ markedly in several respects to the specimen registered as the holotype, although there is no strong reason to doubt that this is the specimen originally described. The original description of the appendix masculina indicates that it has two or three tubercules—this is an artefact, the margins are smooth. The original description of the pleotelson is misleading because it indicates a far more rounded apex and a lack of setae. Plumose setae and sockets are, however, apparent on the margins of the pleotelson, the sockets indicate the former presence of robust setae.

Natatolana natalis is extremely similar to *N. imicola* and *N. rekohu* but has a slightly different morphology of the appendix masculina—the apex is more acute and the notch adjacent to the apex is deeper so that an acute projection occurs proximal to the notch. Because the only specimen of *N. natalis* is in poor condition, further specimens from near the type locality are needed to fully characterize the species and to identify further differences to these species.

Distribution. Off Peru: Peru-Chile Trench. At depths of 2966–2945 m.

Natatolana neglecta (Hansen, 1890)

Synonymy in Keable & Bruce, 1997: 695, figs. 16–18. Additional listings and records of this species are those of Zavodnik & Kovacic (2000, p. 337).

Type material. Syntypes: ♂, 2♀♀, ZMUC CRU148, Gulf of Naples; ♀, ZMUC CRU149, Nice. All examined. • Type locality: Gulf of Naples [as Neapels Golf—c. 40°42'N 14°16'E]; probably Nice (Hansen, 1905) [presumably France, originally as Nizza—c. 43°42'N 7°15.4'E]. All examined.

Material examined. Listed by Keable & Bruce (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.35× as long as body, reaching to three-quarters of the way along pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.84× basal width; anterodorsal depression absent (although in some specimens there is a slight depression this is not equivalent to the distinct and abrupt depression found in species such as *N. pellucida*); anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex not produced, lateral margins converging smoothly to a point; with 10–14 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.09× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.83× the length of the endopod.

Variation. The type specimens have nine to ten robust setae on the pleotelson but other the specimens examined have eight.

Size. Adults to 16 mm.

Remarks. Keable & Bruce (1997) redescribe *Natatolana neglecta*. Hansen (1905) regarded the records of *N. neglecta* by Dollfus (1903), from the mid north Atlantic Ocean and depths of c. 1000–2000 m, as dubious. Keable & Bruce (1997) established the validity of *Natatolana imicola*

(Dollfus) as a distinct species based on the same material. The specimens Dollfus (1903) reported from shallower depths are either *N. neglecta* (IOM 36 0250) or are damaged and mixed with other taxa (IOM 36 0254, *Campagnes de l'Hirondelle et de la Princesse Alice* Station 323) and cannot be accurately identified.

The straight posterolateral margins of the pleotelson, markedly angled to the straight anterolateral margins, is a distinctive feature of *Natatolana neglecta*. This coupled with the well-developed eyes, an incomplete interocular furrow, well-developed coxal furrows on all coxae, absence of penes, appendix masculina morphology, setation and shape of the uropods and setation of the pleotelson, distinguishes this species from all other species of *Natatolana*.

Distribution. *Natatolana neglecta* is known from the west coast of France, the vicinity of Nice and Naples in the Mediterranean and Tyrrhenian Seas, the Atlantic coast of northwestern Africa at about 28°N, and also the Adriatic Sea. At depths of 19–188 m.

The tentative record of Müller (1989), if confirmed, would extend the range of *N. neglecta* to the Levantine Basin of the Mediterranean Sea, (32°0.53'N 34°33.98'E). It has not been possible to locate the specimens and confirm the records of Larwood (1940) from off Egypt, at depths of 42–73 m.

Natatolana nitida (Hale, 1952)

Cirolana nitida Hale, 1952: 25, fig. 1.–Kussakin, 1967: 224.–Carvacho, 1977: 176.–Kensley, 1980: 159.–Kussakin & Vasina, 1982a: 261.–1982b: 329, 335–336.

Natatolana nitida.–Bruce 1981: 958.–1986: 222.–Brandt, 1988: 102.–Brusca *et al*., 1995: 82.–Kensley, 2001: 230.

Type material. Holotype: ♂, 22 mm, SAMA C3279. Allotype: ♀, 24 mm, SAMA C3281. Paratypes: 11, SAMA C3280. All examined. • Type locality: just south of Kerguelen, 49°50'S 69°33'E, [B.A.N.Z.A.R.E. Station 47 First Cruise, 7 Feb. 1930, large rectangular dredge], 150 m.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: weakly developed, indistinct and not extending across the cephalon. *Frontal lamina*: lateral margins sinuate. *Antenna*: c. 0.35× as long as body, reaching to three quarters of the way along pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. Coxa 2 with anteroventral corner produced into an acute tooth. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.89× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle or concave; apex produced into a large point; with 8–10 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.47–0.52× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.96–0.98× length of endopod; margins twisted; broad; apex not at angle to adjacent margins, acute or bluntly rounded. *Uropods*: exopod subequal to endopod, 0.91× the length of the endopod.

Size. Adults to just over 30 mm.

Remarks. *Natatolana nitida* and *N. obtusata* are the only species of *Natatolana* in which males have an excavate medial margin on the endopod of pleopod 2 and a distinctly twisted appendix masculina. *Natatolana nitida* also has a distinct acute tooth on the anteroventral corner of coxa 2 that is otherwise known only in *N. corpulenta*. These characters distinguish *N. nitida* from all other species in the genus. *Natatolana obtusata* is most similar but has the posterodorsal margin of pleonite 4 sinuate, as well as lacking the acute tooth on the anteroventral corner of coxa 2. *Natatolana intermedia* is also similar but has the pleotelson with convex posterodorsal margins and a slender, strongly curved appendix masculina, as well as lacking the acute tooth on the anteroventral corner of coxa 2.

Distribution. Kerguelen Islands, Crozet Islands, Southern Ocean. At depths of 40–334 m (Kussakin & Vasina, 1982b).

Natatolana nukumbutho Bruce & Olesen, 1995

Natatolana nukumbutho Bruce & Olesen, 1995: 212, figs. 1–4.

Type material. Holotype: ♂, 12.3 mm, ZMUC CRU580 (not examined). Paratypes: ♂, 13.2 mm, ZMUC CRU581; 9, ZMUC CRU582 (Bruce & Olesen (1995) list 13 specimens: 2♂♂ and 11♀♀) (not examined); 3, AM P43423, (Bruce & Olesen (1995) list one male and one female) (examined). • Type locality: off Lauthala Bay, Suva, Fiji, 18°13'S 178°29'E, [baited trap], 470 m, [Institute of Marine Research, University of the South Pacific, 23 Jan. 1981].

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4–0.43× as long as body, reaching to between the posterior of pereonite 3 and three quarters of the way along pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.89× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle; apex not produced, lateral margins converging smoothly to a point; with 10–12 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent, vasa deferentia opening flush to surface of sternite 7 (Bruce & Olesen (1995) were unable to discern the openings of the vas deferentia as the internal structure of the specimens appeared somewhat decomposed but distinct penes are absent). *Pleopod 2 appendix masculina*: much shorter than endopod, 0.7–0.87× length of endopod; margins straight; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.86× the length of the endopod.

Variation. The illustration of pereopod 7, provided by Bruce & Olesen (1995), indicates the setae on the anterior margin of the ischium are plumose. Examination of paratype specimens (AM P43423), however, indicates that these setae are slender, without setules. Bruce & Olesen (1995) stated that pleonite 3 does not extend posteriorly beyond the posterior margin of pleonite 5. In the paratype material examined here, however, the posterodistal margin of pleonite 3 does extend beyond the posterior margin of pleonite 5.

Size. Males 11.2 to 13.4 mm, non-ovigerous females 12.2 to 17 mm.

Remarks. *Natatolana nukumbutho* is very similar to *N. carlenae* but differs in having complete coxal furrows on all coxae, a slightly narrower basis on pereopod 7 and slightly narrower posterolateral margins on pleonite 4.

Distribution and ecology. Fiji at a depth of 470 m. Scavenger.

Natatolana obtusata (Vanhöffen, 1914)

Cirolana obtusata Vanhöffen, 1914: 496, fig. 34.–Tattersall 1921: 205.–?Stephensen, 1947: 496, fig. 8.
Natatolana obtusata.–Bruce, 1981: 958.–1986: 222.–Brandt, 1988: 120, figs. 56–60.–Brusca *et al*., 1995: 82.

Type material. Lectotype designated by Brandt (1988): ♂, 38 mm, originally ZMG but now in SIF ZMG 262 (not examined). Paralectotypes: ♂, 27 mm, 5♀♀, 19 mm, 20 mm, 27 mm, 28 mm, 30 mm, SIF ZMG 263; 2♂♂, ZMUC CRU155; 2♀♀, ZMUC CRU156—apparently part of original syntype series from the type locality donated by the Zoological Museum, Berlin, in 1926 (examined). Other possible paralectotypes are: 3♀♀, ZMB 17605; 2♀♀, ZMB 17607—all from type locality (Brandt, 1988) (not examined). • Type locality: off Gauss Station, Posadowsky Bay, Antarctica, 66°2.9'S 89°38.5'E, 385 m, [Deutsche Sudpolarexpedition 1901–1903].

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.75× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle; apex produced into a small point; with 10–14 RS. *Pereopod 2*: propodus with 3–5 RS on palm. *Pereopod 3*: propodus with 4 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.49× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod or just shorter than endopod, 0.9–1× length of endopod; twisted; broad; apex bent laterally slightly, bluntly rounded. *Uropods*: exopod subequal to endopod, 1× the length of the endopod.

Sexual dimorphism. Females may be larger than males.

Size. Females to 37 mm, males to 27 mm.

Remarks. *Natatolana obtusata* and *N. nitida* are the only species of *Natatolana* in which males have an excavate medial margin on the endopod of pleopod 2 and a distinctly twisted appendix masculina. *Natatolana obtusata* most noticeably differs from *N. nitida* in having the anteroventral corner of coxa 2 rounded, not produced into an acute tooth, and in having the posterodorsal margin of pleonite 4 sinuate, not concave. *Natatolana intermedia* is also similar but has a concave posterodorsal margin on pleonite 4.

Distribution and ecology. Antarctica: Gauss Station, Posadowsky Bay, 385 m; Visikoi, S. Sandwich 10–17 m; Bridgeman, S. Sandwich, Antarctic Peninsula, Weddell Sea, 750 m (Brandt, 1988). Scavenger. The anatomy and ultrastructure of the digestive system of this species has been studied by Storch *et al*. (2002).

Natatolana oculata (Vanhöffen, 1914)

Cirolana oculata Vanhöffen, 1914: 499, fig. 36.–Hale, 1937: 17.–1952: 26.–Kussakin, 1967: 224.–?Schultz, 1977: 72, figs. 3–4 [figures labelled *C. albinota*]; 1978: 32.
Natatolana oculata.–Bruce, 1986: 222.–Brandt, 1988: 129, figs. 61–65.–Brusca *et al*., 1995: 82.

Type material. Lectotype designated by Brandt (1988): ♂, 21 mm, ZMB 17617 (not examined). Paralectotypes: ♀, 34 mm, ZMB 17617 (not examined); 2♀♀, ZMUC CRU157—apparently part of the original syntype series from the type locality donated by the ZMB in 1926 (examined). • Type locality: off Gauss Station, Posadowsky Bay, Antarctica, 66°2.9'S 89°38.5'E, 385 m, [Deutsche Sudpolarexpedition 1901–1903].

Material examined. Antarctica: 2♀♀, USNM Acc. No. 247268, Palmer Peninsula, 64°46'S 64°04'W, fish traps, 47.5 m, 5 April, 1963, Staten Island Expedition.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing posteriorly, or lateral margins straight, parallel. *Antenna*: c. 0.3× as long as body, reaching to half way along pereonite 3. *Coxal plates*: furrows moderately developed, on all coxae. Pereonite 1, coxa 2 posterior margins straight or slightly convex, or sinuate. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.84× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins concave; apex produced into a small point; with 8–12 RS. *Pereopod 2*: propodus with 6 RS on palm. *Pereopod 3*: propodus with 4 RS on palm. *Pereopod 7*: basis narrow, width 0.46× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.96× the length of the endopod.

Size. Brandt (1988) states that the maximum length of males is 35 mm and of females 28 mm but also mentions that a paralectotype female is 34 mm.

Remarks. *Natatolana oculata* is similar to *N. meridionalis* and *N. pastorei*. It differs most noticeably from *N. meridionalis* in having the posterolateral margins of the pleotelson distinctly concave and markedly angled to the anterolateral margins (not convex and joining smoothly with anterolateral margins). *Natatolana oculata* differs most noticeably from *N. pastorei* in having the dorsal posterolateral margin of pleonite 2 projecting posterior to the ventral posterolateral margin (not projecting subequal to the ventral margin).

The material of Schultz (1977) from southern Argentina is discussed under remarks for *N. meridionalis*.

Distribution and ecology. Magellan Strait, South Shetland Islands, Antarctic Peninsula and Weddell Sea (Brandt, 1988); possibly southern Argentina. At depths of 43.5–385 m. Scavenger.

Natatolana pallidocula (Kussakin & Vasina, 1982)

Cirolana pallidocula Kussakin & Vasina, 1982a: 262, figs. 1, 2.–1982b: 329, 334.
Natatolana pallidocula.–Bruce, 1986: 222.–Brusca *et al.*, 1995: 82.–Kensley, 2001: 230.

Type material. Holotype: ♂, 10.8 mm, ZIAS 1/71 227 (not examined, an attempt to obtain the only known specimen, from the Zoological Institute of the Academy of Science, St. Petersburg, was unsuccessful). • Type locality: Kerguelen Islands, 49°18'S 71°12'E, 310 m.

Diagnosis. Details regarding the interocular furrow, labrum, coxa 2, number of robust setae on the pleotelson, setation and size of the pereopod articles, and penes are unknown. *Eyes*: well developed (although described as hardly distinguishable because they lack pigment, this may be due to preservation as the ommatidia are apparently well developed). *Antenna*: c. 0.35× as long as body, reaching to middle of pereonite 3. *Coxal plates*: furrows variously developed, coxa 2 with a short straight furrow, coxae 3–6 with strongly developed furrows and coxa 7 apparently without furrows. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle or concave; apex produced into a large point; RS present. *Pereopod 7*: basis narrow; posterior margin with setae on distal two-thirds. *Pleopod 2 appendix masculina*: just shorter than endopod; margins straight; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.9× the length of the endopod.

Size. The only known specimen is a male of 10.8 mm.

Remarks. *Natatolana pallidocula* is known only from the holotype. This species appears to be very similar to *N. corpulenta*. The eyes in *N. pallidocula* are, however, apparently longer, with more ommatidia in the horizontal row, than those of *N. corpulenta*. It is unclear from the original illustrations but the ventral anterior tooth on coxa 2, characteristic of *N. corpulenta*, may also be present in *N. pallidocula*.

Distribution. Kerguelen Islands, Southern Ocean. At a depth of 310 m.

Natatolana paranarica n.sp.

Figs. 36–37

Type material. HOLOTYPE: ♂, 31 mm, NMNZ. PARATYPES: 3♂♂, 5♀♀, manca, NMNZ Cr 4992; ♂, ♀, QM W18897. • Type locality: Palliser Bay, off Carls Beach, North Island, New Zealand, [c. 41°S 175°E], 5.5m, [14 Jan. 1986].

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, forming a ridge that extends across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.48× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows variously developed, incomplete on coxae 2–3, absent on coxae 4–7. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.9× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 10–14 RS. *Pereopod 2*: propodus with 0–2 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.92× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod longer than endopod, 1.08× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.8× width. Colour cream/yellow in alcohol. Chromatophores absent. *Eyes*: with 14 ommatidia in horizontal diameter; with 11 ommatidia in vertical diameter; round; lacking pigment in alcohol. *Frontal lamina*: length c. 3.9× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta and 3 penicillate setae; article 3 short, subequal to article 1. Flagellum 16-articulate. *Antenna*: peduncular article 4 with 6 SS medially on posterolateral margin, 2 SS near posterodistal angle and 4 SS at anterodistal angle; article 5 with 2 pappose setae at posterodistal angle, 4 SS and 1 penicillate seta at anterodistal angle. Flagellum 28-articulate. *Mandible*: setal row with 21 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 15 SS and 8 PS; middle lobe with 18 SS. *Maxilliped*: endite with 2 coupling hooks, 1 PS and 2 SS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1, 1 short curved furrow on lateral margin of pereonites 2–3, 1 short medial furrow on lateral margins of pereonites 4–7; pereonite 1 longest, 2–6 subequal, 7 shortest. *Coxae*: pereonite 1 and coxa 2 with rounded posteroventral corners, coxa 3 with square posteroventral corner, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex, PS present. Ischium anterior margin with SS; posterior margin without RS, PS present. Merus anterior margin with SS; posterior margin without RS (9 submarginally), SS present. Carpus posterior margin without RS, SS present. Propodus longer than carpus; posterior margin with 5 RS, SS present. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 4 RS, PS on distal three-quarters. Exopod medial margin convex, with 4 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 8 RS, PS along entire length.

Variation. Several of the paratypes have one or two robust setae on the palm of pereopod 2 but this is not a consistent feature. The holotype has 11 robust setae on the pleotelson. Robust setal counts from margins of paratypes (n=10): pleotelson: damaged (20%); 5:6 (20%); 6:6 (30%); 6:7 (30%). Endopod, medial: 6 (70%), 5 (30%); lateral: 2 (10%), 3 (30%), 4 (60%). Exopod medial: 3 (20%), 4 (60%), 5 (20%); lateral: 7 (10%), 8 (30%), 9 (40%), 10 (20%).

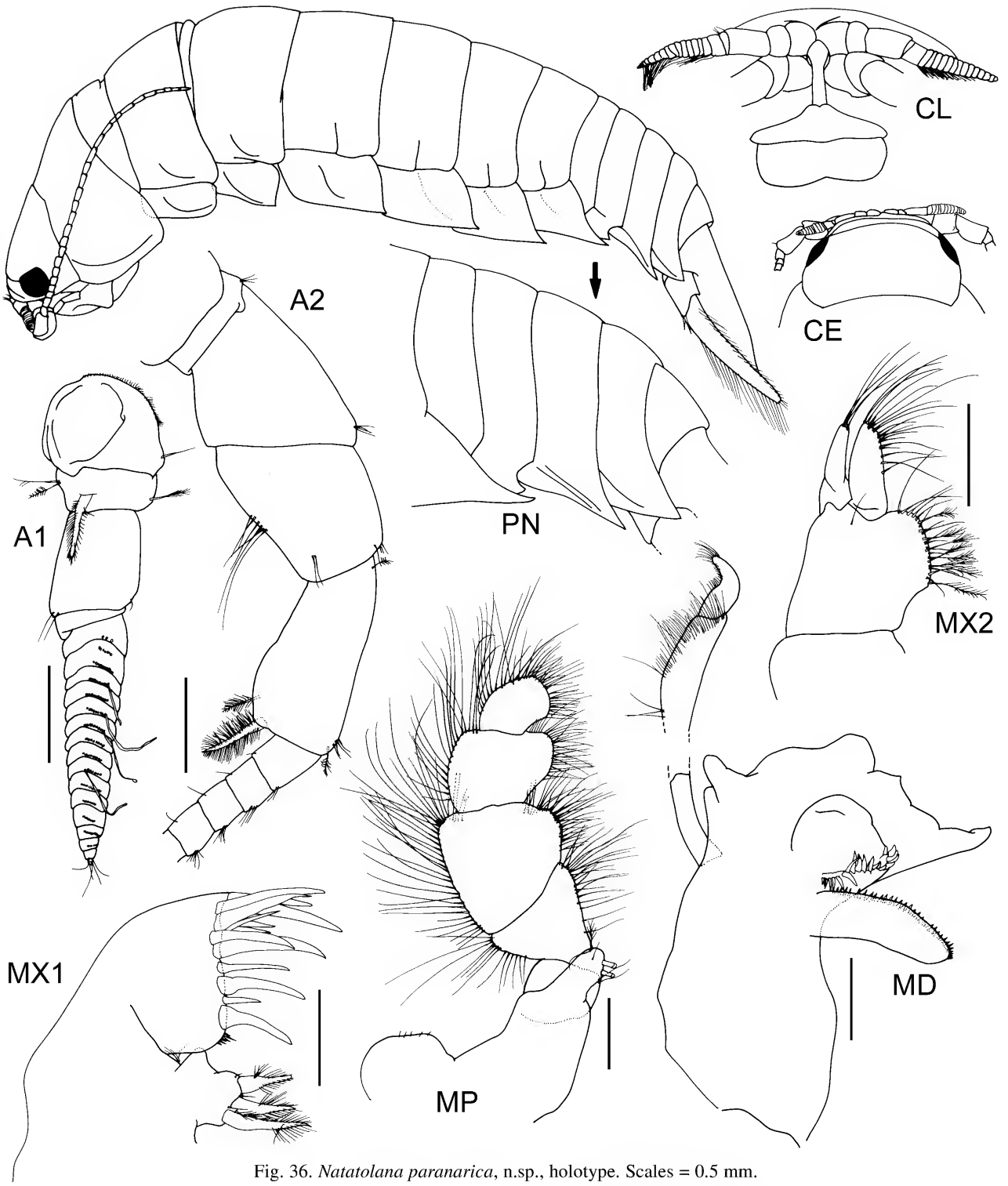

Fig. 36. *Natatolana paranarica*, n.sp., holotype. Scales = 0.5 mm.

Size. Adults to 31 mm.

Etymology. Refers to the similarity this species has to *Natatolana narica*.

Remarks. *Natatolana paranarica* is almost identical to *N. narica* but differs in that the posterolateral margins of the pleotelson meet at an acute angle, rather than being broadly rounded; the uropod endopod medial margin is smoothly convex, not sinuate; the ventral margin of the posterior coxae is straight not sinuate; there are slender setae at the uropod endopod and exopod apices that are shorter than the length of these rami, rather than being as long as them. *Natatolana paranarica* and *N. narica* are the only species of *Natatolana* in which the uropod exopod is distinctly longer than the endopod. The uropod exopod is as long as the endopod in *N. endota* but that species differs in many characters, including having only four robust setae on the pleotelson and antennae that are longer than the body.

Distribution. New Zealand: known only from the type locality. At a depth of 5.5 m.

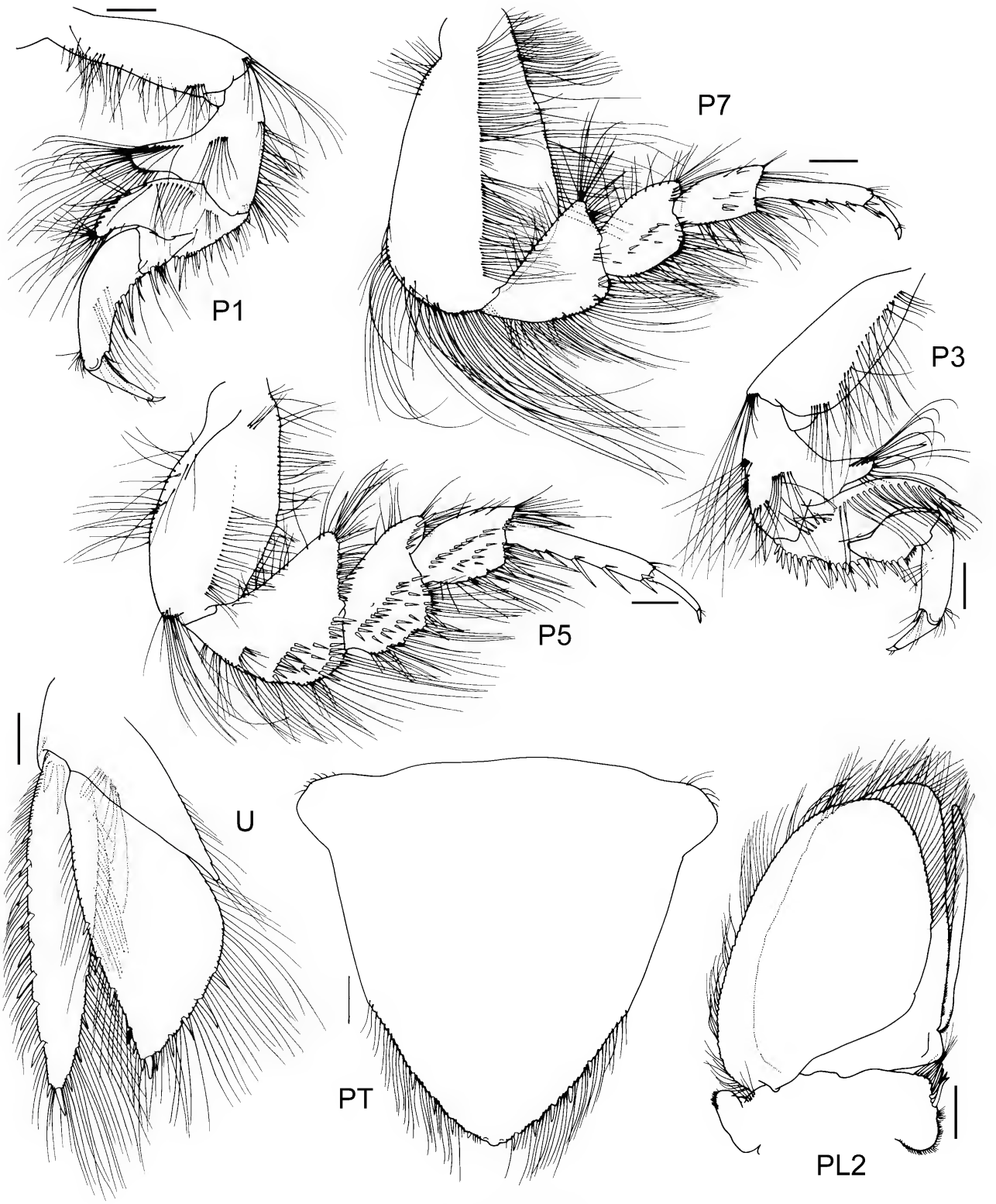

Fig. 37. *Natatolana paranarica*, n.sp., holotype. Scales = 0.5 mm.

Natatolana pastorei (Giambiagi, 1925)

Cirolana magellanica Pfeffer, 1887: 58, *nomen nudum*.–Hansen, 1890: 357.–Bruce, 1986: 218.–Wägele & Bruce, 1989: 95
Cirolana pastorei Giambiagi, 1925: 4, pl. 1, pl. 3, fig. 3.
Natatolana pastorei.–Bruce, 1981: 958.–1986: 97, 222.–Wägele & Bruce, 1989: 95.–Brusca *et al.*, 1995: 82.–Lorenti & Mariani, 1997: 255.
?*Cirolana oculata*.–Schultz, 1977: 72, figs. 3–4 [figures labelled *C. albinota*]. [possible mis-identification of *Natatolana oculata* Vanhöffen, 1914].
Not *Cirolana pastorei*.–Monod, 1931: 22 [mis-identification = *Natatolana* sp.].

Type material. Syntypes: 9, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires Nr 12690 (not examined). • Type locality: San Sebástian, Tierra del Fuego [c. 53°9'S 68°18'W].

Material examined. **Chile**: ♀, ♂, AM P47134, Fiordo Quintupeu, 42°10'S 72°25'W, A. Carvacho; ♂, USNM Acc. No. 288382, off south tip of Vancouver Island, 51°27.5'S 74°03'W, epibenthic dredge, 700–920 m, D.L. Pawson, 10 Oct. 1969, HERO Cruise 69-5 stn 213; ♂, USNM Acc. No. 288382, 53°31'S 70°33'W, 270 m. **South Georgia**: 2♂♂, ♀, ZMUC CRU132, 54°27.3'S 35°47.5'W, 50 m.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.92× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 10–16 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis broad, width 0.54× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on distal half. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins straight; slender; apex recurved, bent slightly medially, tapered to a finely acute point. *Uropods*: exopod subequal to endopod, 1 × length of endopod.

Variation. Wägele & Bruce (1989) state that the antennule flagellum is not much longer than the peduncle. Their illustration, however, shows the peduncle longer than the flagellum and this is the case in the material examined. The specimens from southern Chile (AM P47134) have the apex of the pleotelson less produced than in other material examined. One specimen from southern Chile (USNM Acc. No. 288382) has only 10 robust setae on the pleotelson rather than the 12–16 recorded by Wägele & Bruce (1989).

Size. Immature adults 27–34 mm, males 30.5–33 mm (Wägele & Bruce, 1989).

Remarks. *Natatolana pastorei* is similar to *N. meridionalis* and *N. oculata* but differs most noticeably in having the dorsal posterolateral margin of pleonite 2 projecting subequal to the ventral posterolateral margin (not projecting posterior to the ventral margin), pereonite 1 and coxa 2 with straight or slightly convex posterior margins (never sinuate) and the appendix masculina tapered to a finely acute point (not bluntly rounded).

The possible record from southern Argentina by Schultz (1977) (as *Cirolana oculata*, figures labelled *C. albinota*) is discussed under remarks for *N. meridionalis*.

Distribution and ecology. Straits of Magellan; South America: between Hale Cove, Argentina to Punta Arenas, Chile and from San Sebastián, Argentina. In shallow sublittoral sediments (Wägele & Bruce, 1989). New records reported here are from the vicinity of South Georgia and to depths of 920 m. Scavenger.

Natatolana pellucida (Tattersall, 1921)

Cirolana pellucida Tattersall, 1921: 206, pl. II figs. 4–10.–Nierstrasz, 1931: 158.–Hurley, 1957: 11.–1961: 267.
Natatolana pellucida.–Bruce, 1981: 958.–1986: 76, figs. 49, 50.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 152.

Type material. Syntypes: ♂, 7.5 mm, 2♀♀, 11.3, 12.0 mm, BMNH 1921.11.29.22-24 (measurements of Bruce (1986), examined and newly measured here as—undissected female, 11 mm, partially dissected ♂, 9.5 mm and fully dissected female, 12 mm); many specimens, BMNH 1921.11.29.25-44. All examined. • Type locality: off Three Kings Island, New Zealand [c. 34°14'S 172°12'E, British Antarctic (*Terra Nova*) Expedition Station 130], surface.

Material examined. **Queensland**: series from off East Fitzroy Reef, AM P47619–47622; 29, 23°34.92'S 152°11.76'E, 58 m, 16–17 Jun. 1993, SEAS QLD-952; 1, 23°32.53'S 152°16.45'E, 105 m, 16–17 Jun. 1993, SEAS QLD-956; 8, 23°32.16'S 152°17.98'E, 203 m, 16–17 Jun. 1993 SEAS QLD-959; 7, due east of Mooloolaba, 26°36.21'S 153°34.90'E, 116 m, 2–3 Aug. 1994, SEAS QLD-1126.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.3× as long as body, reaching to between the posterior of pereonite 2 and half way along pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.8× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 8–12 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth (Bruce (1986) describes it and illustrates it (from a topotype male) as relatively narrow. In the syntype female examined here it is broader), width 0.48–0.53× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.06× length of endopod; slender; margins sinuate; apex recurved, bent slightly medially, acute. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Variation. There is a variation in the number of robust setae found on the pleotelson margins. For the syntypes Tattersall (1921) describes and illustrates 12 robust setae while Bruce (1986) describes and illustrates only 10. In BMNH 1921.11.29.22-24 the undissected female syntype has 11 robust setae, the male has nine (and appears damaged on side with only three) and the fully dissected female has 10.

In a subsample of ten syntype specimens from BMNH 1921.11.29.22-24, 30% had 10 robust setae, 60% had 11 and 10% had 12. The material from off East Fitzroy Reef, Australia (AM P47619–47622) consistently had only eight robust setae on the margins of the pleotelson. Male syntype specimens in BMNH 1921.11.29.22-24, 25-44, have conspicuously elongated robust setae on the merus of pereopods 4–6 but do not have the elongated robust setae on the merus of pereopods 1–3 that are illustrated by Bruce (1986) from Australian material.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Largest female 12.0 mm, largest male 8.7 mm, largest manca 5.1 mm, smallest adult female 4.1 mm.

Remarks. *Natatolana pellucida* is most readily distinguished from similar species by details of the pleotelson and uropods, presence of well-developed eyes, rounded posteroventral margins of pereonite 1 and coxa 2 and relatively short propodus of pereopod 5. This species is most similar to *N. galathea* but has a relatively narrow pleotelson and uropod endopod compared to it.

Distribution and ecology. Australia: Moreton Bay north to Gladstone Queensland, New South Wales, Bass Strait, Tasmania. New Zealand, Campbell Island. Recorded from surface plankton to a depth of 450 m. Scavenger.

Natatolana pilula (Barnard, 1955)

Figs. 38–40

Cirolana pilula Barnard, 1955: 54, fig. 26a–c.–Kensley, 1975: 39.–1978: 69, fig. 28H.

Natatolana pilula.–Bruce 1981: 958.–1986: 8, 222.–Brusca *et al*., 1995: 82.–Kensley, 2001: 230.

Type material. Syntypes: 3 specimens, SAM A-43144. According to Barnard (1955) "including male but no ovigerous female". All examined. The material registered as the types has been largely dismembered. One specimen (including pereonites 2–7, pleon and pleotelson), however, has ooestegites and developing embryos. The remaining specimens cannot be sexed. The pleopod 2 with the appendix masculina figured by Barnard (1955) is not present. None of the type material is in good enough condition to use for a full redescription. • Type locality: False Bay, South Africa, 34°17'06"S 18°39'02"E and 34°12'08"S 18°36'05"E, 46–62 m.

Material examined. **South Africa**: ♂, 10 mm, SAM-A14532, False Bay, 34°12.5'S 18°37'E, 15 May 1961, Sta No: FAL 414V.

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.2× as long as body, reaching to just posterior of pereonite 1. *Coxal plates*: furrows variously developed, strong but incomplete on coxae 2–4, complete on coxae 5–7. *Pleonite 4*: apex broadly rounded. *Pleotelson*: broad, length 0.67× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins broadly rounded; apex truncate; RS absent. *Pereopods 2–3*: propodus without RS on palm. *Pereopods 5–7*: propodus short and robust on each pereopod. *Pereopod 7*: basis broad, width 0.58× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.99× length of endopod; margins straight or sinuate; slender; apex bent laterally slightly, serrulate with a minute digitiform process. *Uropods*: exopod slightly shorter than endopod, 0.8× the length of the endopod.

Additional descriptive characters. *Body*: length c. 2.5× width. Colour cream to white in alcohol. Chromatophores absent. *Cephalon*: submarginal cephalic furrow moderately developed, does not run entire length of anterior margin. *Eyes*: with 7 ommatidia in horizontal diameter; with 9 ommatidia in vertical diameter; ovate; colour deep red in alcohol. *Frontal lamina*: length c. 3× basal width; apex expanded, anterior margin angled. *Antennule*: short, just reaching pereonite 1. Peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 very long, subequal to or longer than the combined lengths of articles 1 and 2. Flagellum 10-articulate. *Antenna*: peduncular article 4 with long SS projecting from posterolateral margin; article 5 with 2 conspicuous pappose setae at posterodistal angle. Flagellum 15-articulate. *Mandible*: setal row with 13 RS. *Maxillule*: medial lobe with 3 large robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 6 SS; medial lobe with 5 SS and 6 PS; middle lobe with 15 SS. *Maxilliped*: endite with 2 coupling hooks, and 5 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on the lateral margins of pereonite 1 and 1 weakly developed furrow on lateral margins of pereonites 2–7; pereonite 1 longest, 2–5 subequal, 6–7 progressively shorter. *Coxae*: pereonite 1, coxae 2–4 with rounded posteroventral corners, coxa 5 with a short square corner, coxae 6 and 7 with broad, acute, posteroventral corners. *Pleonites*: 1 concealed by pereonite 7, 2–5 visible. *Pleonite 2*: not produced. *Pleonite 3*: subacute. *Pleotelson*: PS restricted to apex. *Pereopod 7*: basis anterior margin straight; medial carina with PS along entire length; posterior margin convex, posterior margin SS present. Ischium anterior margin with non-RS absent; posterior margin with 2 RS (submarginal), PS present. Merus posterior margin with 8 RS, SS present. Carpus posterior margin with 1 RS, SS absent. Propodus subequal to carpus; posterior margin with 3 RS, SS present. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture absent on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod subcircular; medial margin rounded, with 3 RS, PS along entire length; apex with 3 RS; lateral margin straight, with 1 RS, PS on distal three-quarters. Exopod medial margin convex, with 1 RS, PS present on distal half; apex rounded, with 3 RS; lateral margin convex, with 2 RS, PS on distal quarter.

Size. 10–11 mm (Barnard, 1955; Kensley, 1978; this study).

Remarks. The material examined matches the original description and illustrations of *Natatolana pilula* by Barnard (1955) except that chromatophores are absent, whereas the original description mentions pinkish or greyish speckles.

The following characters are most useful in distinguishing *Natatolana pilula* from other species within the genus; the short antenna, the shape of the posterolateral margins of pleonites 3 and 4, the shape and setation of the pleotelson and uropods; and the morphology of the appendix masculina apex.

Distribution. South Africa: Lambert's Bay to Natal. At depths of 18–66 m (Barnard, 1955; Kensley, 1978; Bruce, 1986).

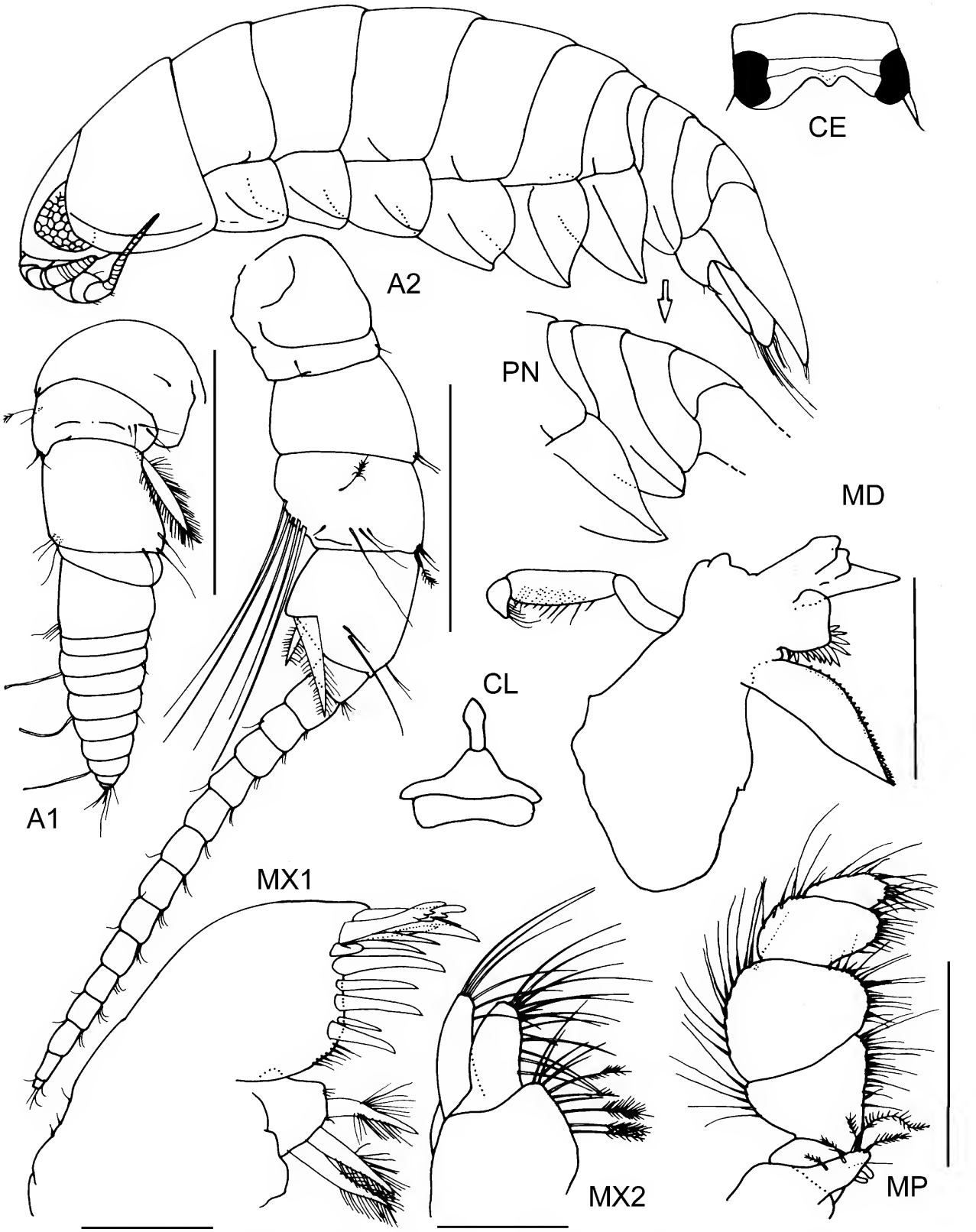

Fig. 38. *Natatolana pilula*, male SAM A-14532. Scales for MD, MP = 0.5 mm, for MX1, MX2 = 0.2 mm, for A1, A2 = 0.5 mm.

Natatolana prolixa Bruce, 1986

Natatolana prolixa Bruce, 1986: 64, figs. 40, 41.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 152.

Type material. Holotype: ♂, 21.0 mm, QM W6738 (examined). • Type locality: off Hay Point, Mackay, Queensland, Australia, 21°17'S 149°18'E.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 1.5× as long as body, reaching to beyond pleotelson. *Coxal plates*: furrows variously developed, indistinct furrows on coxae 2–3 only. *Pleonite 2*: ventral posterolateral margin acute,

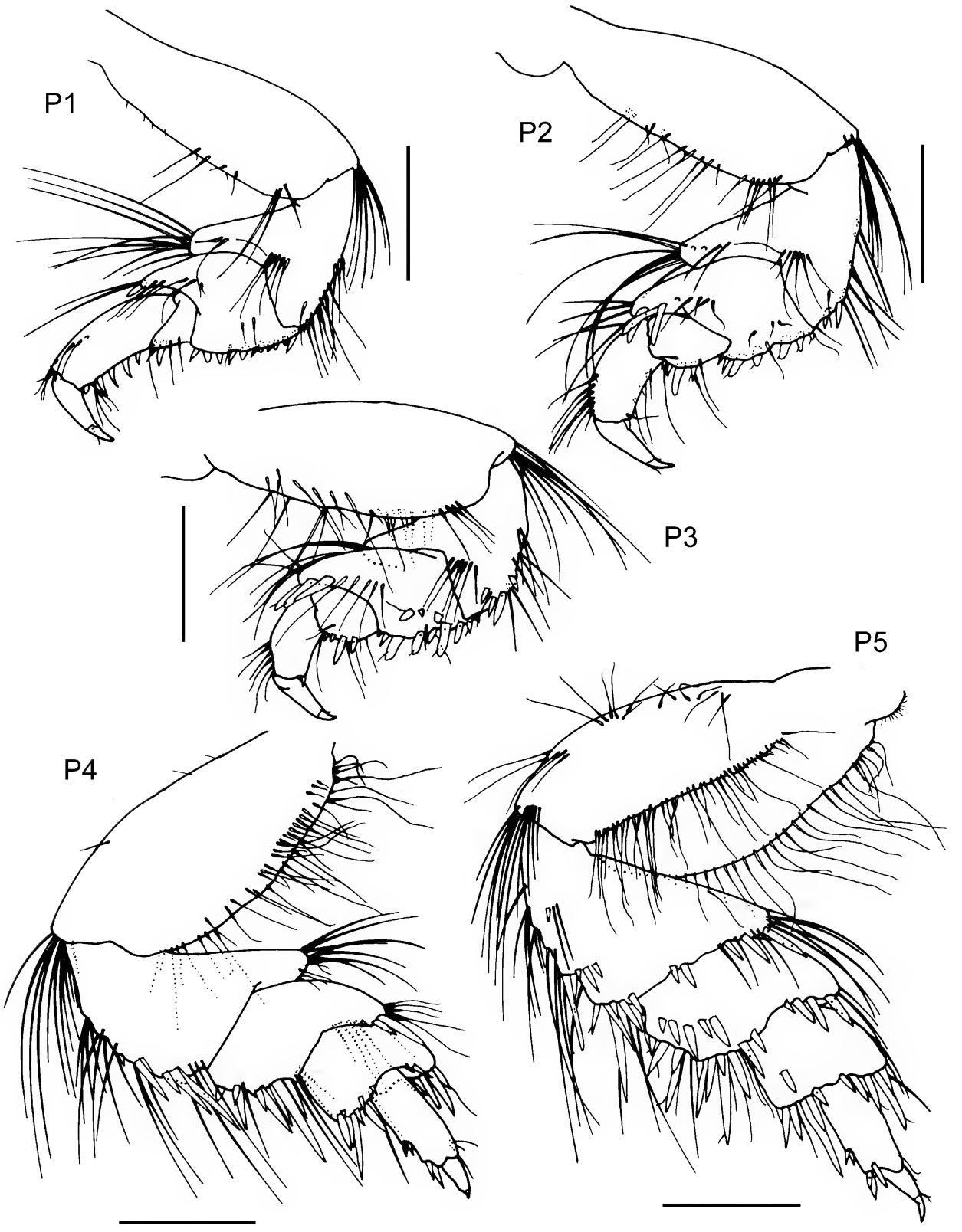

Fig. 39. *Natatolana pilula*, male SAM A-14532. Scales = 0.5 mm.

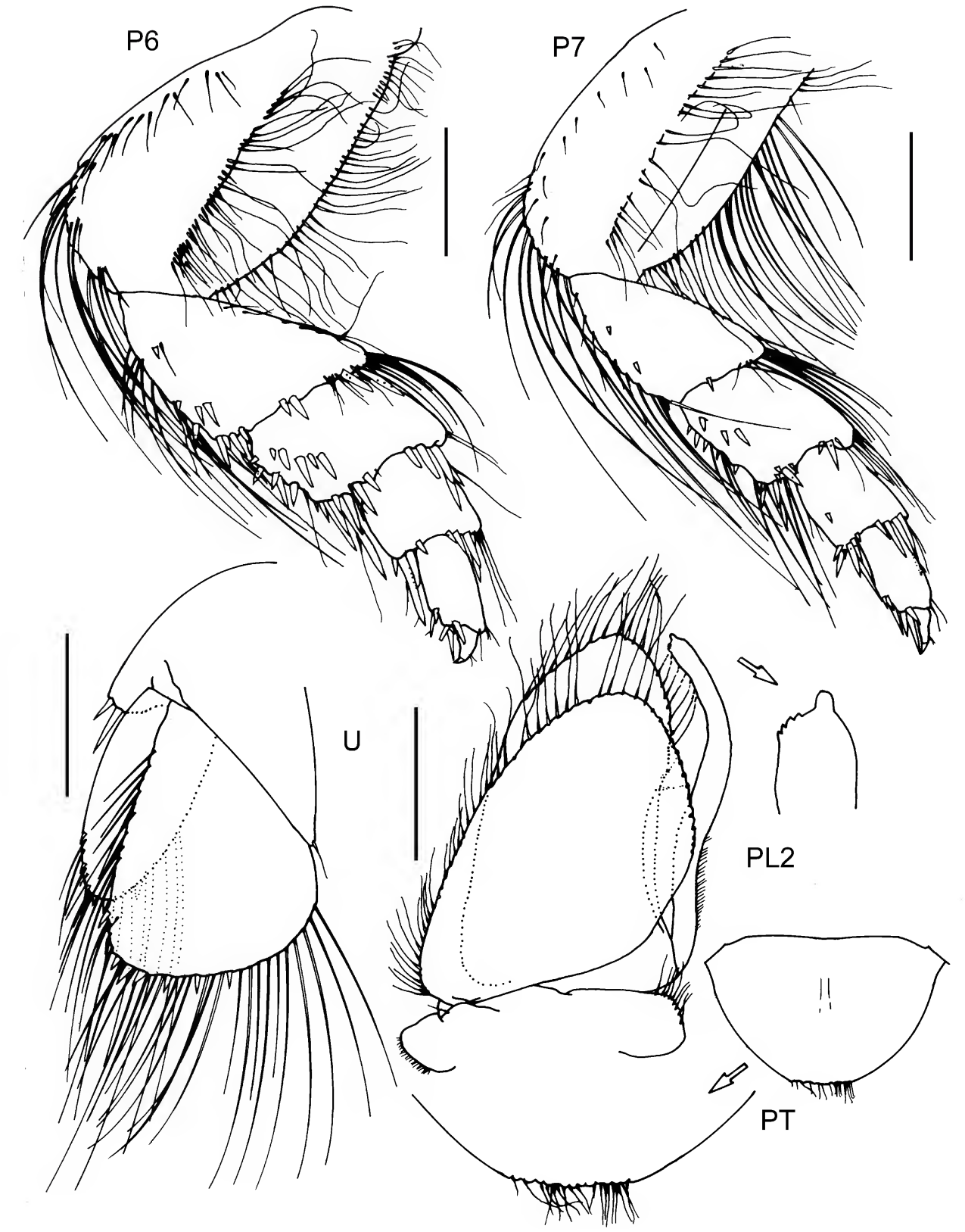

Fig. 40. *Natatolana pilula*, male SAM A-14532. Scales = 0.5 mm.

formed into long curved process. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.75× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins concave; apex produced into a large point; RS absent. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: present (although the vas deferens are described as opening flush to the sternite surface by Bruce (1986), distinct penial processes are evident in the type material). *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; slender; margins straight; apex not at angle to adjacent margins, acute. *Uropods*: exopod subequal to endopod, 0.95× the length of the endopod.

Sexual dimorphism. Unknown.

Size. Adults to 21 mm.

Remarks. The long antennae and sinuate margins of the pleotelson that lack robust setae separate *Natatolana prolixa* from all other species in the genus.

Distribution. Australia: Hay Point, Mackay, Queensland. At depths of 15–21 m.

Natatolana rekohu Bruce, 2003

Natatolana rekohu Bruce, 2003: 4, figs. 1–4.

Type material. Holotype, NIWA H831, male (19.5 mm). Paratypes, NIWA P1380, 5♂♂ (18.5, 20.0, 20.5, 23.3, 24.0 [dissected] mm), 13♀♀ (non-ovigerous 17.5–26.5 mm), 3 mancas (8.5, 9.1, 12.0 mm). None examined. • Type locality: Chatham Rise, 46°38.24'S 178°31.39'E, 2769 m.

Material examined. 10, AM P65202, from type locality.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.19× as long as body, reaching to middle of pereonite 3. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 2*: ventral posterolateral margin not produced. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.7× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point, or rounded; with 12–18 RS. *Pereopod 2*: propodus with 3–7 RS on palm. *Pereopod 3*: propodus with 4 RS on palm. *Pereopod 7*: basis narrow, width 0.39× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on more than proximal half. *Penes*: present. *Pleopod 2 appendix masculina*: just shorter than endopod, 0.9× length of endopod; margins very strongly curved laterally; broad; apex not at angle to adjacent margins, club shaped with a lateral notch. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod.

Size. Males 18.5–24.0mm, females 17.5–24.5mm, both with a mean of 21mm; mancas 8.5–12.0mm.

Remarks. *Natatolana rekohu* is most similar to *N. imicola*. It can be distinguished from that species by (in *N. rekohu*) the greater number of robust setae on the propodal palm of pereopods 1–3 and the (generally) greater number of robust setae on the margins of the pleotelson and uropods. These two species can be separated from other species of *Natatolana* in which the eyes are vestigial or absent by: the presence of coxal furrows on all coxae; the distinctive club shaped appendix masculina of male specimens; and the ischium of pereopod 3 having the anterodistal angle not weakly produced relative to that of pereopods 1–2.

Distribution and ecology. Chatham Rise, southeast of New Zealand. At a depth of 2799 m. Scavenger.

Natatolana rossi (Miers, 1876)

Figs. 41–42

Cirolana rossi Miers, 1876a: 228.–1876b: 109. pl. 3, fig. 3.–Hutton, 1879: 340.–Filhol, 1885: 453, 499.–Hansen, 1890: 355.–Thomson & Chilton, 1886: 154.–Chilton, 1909: 606, 651.–Nierstrasz, 1917: 91, pl. 13, figs. 11–17.–1931: 158.–Stephensen, 1927: 361.–Hurley, 1961: 267.–Kussakin, 1967: 223.–Ellis, 1981: 123.

Natatolana rossi.–Bruce, 1981: 958.–1986: 53, 93, 97, 222.–Brusca *et al.*, 1995: 82.

Cirolana hirtipes.–Filhol, 1885: 455, 499, pl. 53 fig. 6.–Nierstrasz, 1931: 158.–Hurley, 1961: 267 [mis-identification, not *N. hirtipes* (Milne Edwards, 1840)].

Not *Cirolana rossi*.–Hale, 1952: 24 [mis-identification = *N. matong* Bruce, 1986].

Type material. Lectotype: designated here, ♂, 18 mm, BMNH 1844:3. Paralectotypes: all BMNH, 2, 1843: 70; 6, 1844: 3; 1, 1848: 80; 2, 1856: 33. Details as per the list of Ellis (1981) except the material presented by Lieut. A. Smith has the label: "Rendezvous Cove, Auckland Island, 'Erebus'—Antarctic Expedition" and has registration number: 1843:70, not 1856:33. All examined. • Type locality: originally New Zealand, [c. 40°S 175°E] and Auckland Islands, New Zealand, [50°35'S 166°E], now restricted to Auckland Islands, New Zealand.

Material examined. **New Zealand**: 4, NMNZ Cr 9199, west of Rangitikei River mouth, 40°16'S 174°58.5'E, 75 m, RV *Acheron*, 2 Mar. 1976; 1, NMNZ Cr 9197, between West Entry Point and Duffers Reef, Pelorus South, 40°57.5'S 174°01.5'E, 29 m, RV Acheron, 5 Mar. 1976; 4, NMNZ Cr 9201, south of Mana Island, 41°10'S 177°43'E, 37–53 m, 21 Oct. 1969; many, QM W10261, Tasman Bay, 41°17.55'S 173°16.97'E, trap, 14 m, 2 May 1971, NIWA stn K179(4); 36, NMNZ Cr 4997, Kaikoura, [42°23'S 173°41'E], feeding on crayfish bodies in hagfish trap, Jul. 1987; 20, NMNZ 4998, Kaikoura, baited trap, 10 Sep. 1974. 10, NMNZ 9200, North Otago, on *Squalus acanthus*, 27–33 m, J. Graham, Oct. 1961; 10, NMNZ Cr 4999, Auckland Island, [50°35'S 166°E], in crab pots, 55 m, L.D. Ritchie, 11 Feb. 1970.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon; produced medially. *Frontal lamina*: lateral margins straight, narrowing anteriorly, or medially constricted. *Antenna*: c. 0.35–0.5× as long as body, reaching to between the posterior of pereonite 3 and pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex forming a broad acute point, or slightly rounded. *Pleotelson*: broad, length 0.8× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle or convex;

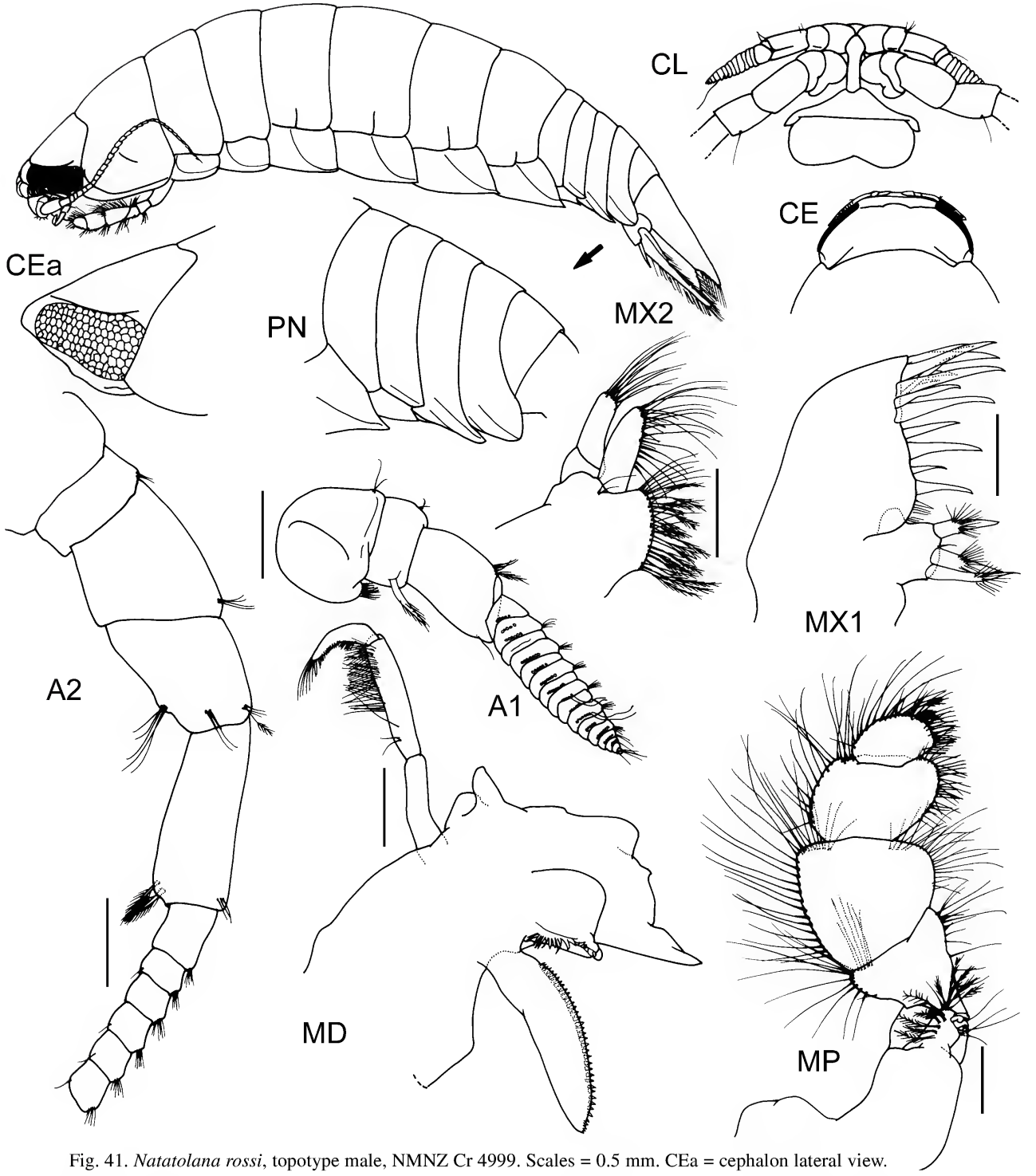

Fig. 41. *Natatolana rossi*, topotype male, NMNZ Cr 4999. Scales = 0.5 mm. CEa = cephalon lateral view.

apex not produced, lateral margins converging smoothly to a point; with 10–16 RS. *Pereopod 2*: propodus with 3 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis broad, width 0.64× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.96× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.94× the length of the endopod.

Additional descriptive characters. Based on a topotype, male, 36 mm, NMNZ Cr.4999. *Body*: length c. 2.7× width. Colour yellow or salmon-pink in alcohol. Chromatophores absent. *Eyes*: with 18 ommatidia in horizontal diameter; with 8 ommatidia in vertical diameter; rectangular; colour tan in alcohol. *Frontal lamina*: length c. 4.2× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 short, subequal to article 1. Flagellum 16-articulate. *Antenna*: peduncular article 4 with 1 patch of 6 SS on posterolateral margin, 2 SS distomedially, 3 PS and 1 penicillate setae at anterodistal angle; article 5

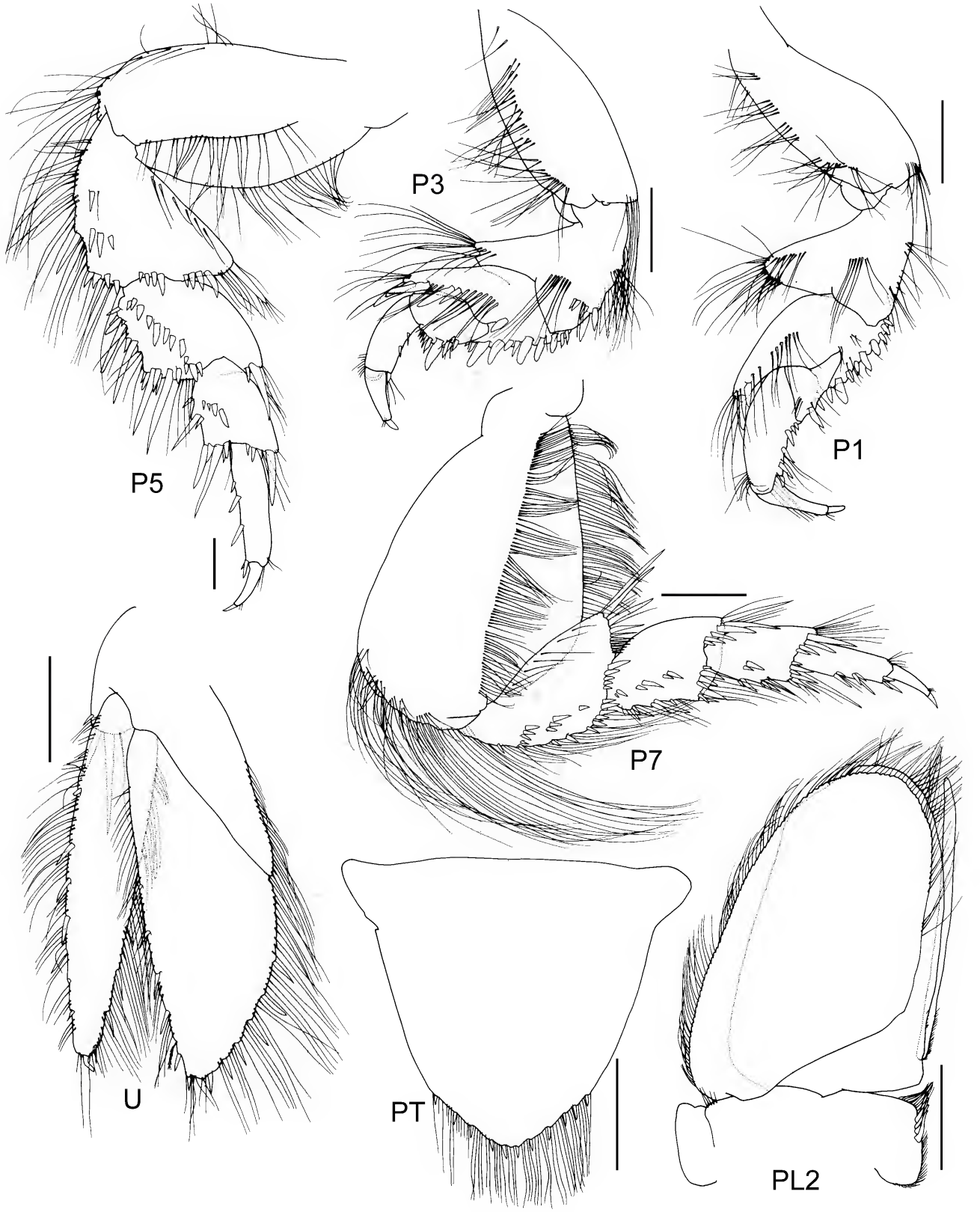

Fig. 42. *Natatolana rossi*, topotype male, NMNZ Cr 4999. Scales = 1.0 mm.

with 2 pappose at posterodistal angle, 3 SS at anterodistal angle. Flagellum 34-articulate. *Mandible*: setal row with 19 RS. *Maxillule*: medial lobe with 3 large robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 12 SS; medial lobe with c. 12 SS and 23 PS; middle lobe with 26 SS. *Maxilliped*: endite with 5 coupling hooks, 1 SS and 12 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of 4–7; pereonites 1 and 5 subequal in length and longest,

pereonites 4, 6–7 subequal and longer than 2–3 which are subequal. *Coxae*: pereonite 1 and coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin convex; medial carina with PS along entire length; posterior margin convex. Ischium anterior margin with SS; posterior margin with 4 RS (and 8 submarginally), PS present. Merus posterior margin with 5 RS (and 6 submarginally), SS present. Carpus posterior margin with 6 RS (and 2 submarginally), SS present. Propodus subequal to carpus; posterior margin with 6 RS, SS present. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture feebly developed (sutures present at margins but not medially) on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 5 RS, PS on distal three-quarters. Exopod medial margin convex, with 3 RS, PS on distal three-quarters; apex acute, with 2 RS; lateral margin convex, with 8 RS, PS along entire length.

Variation. There is considerable variation in the number of robust setae on the pleotelson and uropods of individuals within all samples examined. There are also some differences between samples; specimens in BMNH 1856:33 (New Zealand), QM W10261 (Tasman Bay), NMNZ Cr 9197, 9199, 9200 and 9201 (Pelorus South, Rangitikei River, Otago, Mana Island, respectively), tend to have a greater number of robust setae on the pleotelson and uropods than specimens in other samples. A comparison (below) of 10 specimens from each of the samples NMNZ Cr 4999 (Auckland Island) and 9200 (Otago) indicates this, figures for Cr 9200 are in square brackets. Pleotelson: 11 (20%), 12 (60%), 13 (20%), [14 (100%)]. Endopod, medial: 5 (30%), 6 (60%) [20%], [7 (80%)], 8 (10%); lateral: 4 (20%), 5 (40%), 6 (40%) [60%], [7 (30%)], [8 (10%)]. Exopod, medial: 3 (20%), 4 (80%) [10%], [5 (70%)], [6 (20%)]; lateral: 8 (30%), 10 (10%) [20%], 11 (50%) [40%], [12 (40%)]. Because the ranges tend to overlap and no other consistent feature (such as the variation in pleotelson shape as noted in the diagnosis and below) could be found to correlate with these variations, and separate the specimens in these samples, it was concluded that a single variable species is represented. The full variation in setal counts is as follows; pleotelson 10–16, uropod endopod medial margin 5–8, lateral margin 4–8, uropod exopod medial margin 3–6, lateral margin 8–12.

The length of the antenna also varies, on some specimens it reaches to the posterior of pereonite 4 and is 0.5× the length of the body, while in the material described and the lectotype selected here (see below) it reaches to the posterior of pereonite 3 and is c. 0.35× the length of the body. The number of flagella articles in the antennae also ranges from 26–36. Furthermore, in some specimens the anterolateral and posterolateral margins of the pleotelson are relatively straight compared to the material illustrated here. In the material examined the number of coupling hooks on the maxilliped endites ranged from two to five. Smaller specimens have fewer articles in the antennular and antennal flagella, and fewer coupling hooks on the maxilliped endite.

The lectotype has 11 robust setae on the pleotelson, six on the uropod endopod medial margin, 6 on the uropod endopod lateral margin, four on the uropod exopod medial margin and 12 on the uropod exopod lateral margin. In the lectotype the antennae extend to just beyond pereonite 3 and the posterolateral margins of the pleotelson are only slightly convex and distinctly angled to the anterolateral margins, which are relatively straight.

Size. Lengths of 25 mm, 26 mm and 21 mm have previously been recorded (Miers, 1876a, b; Nierstrasz, 1917; Kussakin, 1967). In the material examined here adults ranged from 18 mm up to 36 mm.

Remarks. Because of the large number of syntypes and the variation among them, a male (BMNH 1844:3, Auckland Is., Antarctic Expedition, Presented by Capt. James Clarke Ross) is selected here as a lectotype for *Natatolana rossi* to avoid future taxonomic confusion when identifying this species. The remaining type specimens become paralectotypes. A topotype that has been closely compared to the types is illustrated here, and used for the description of characters additional to the diagnosis, because the type specimens are fragile and are damaged so that they lack many setae.

Natatolana rossi is extremely similar to *N. hirtipes* in most features, as noted by Chilton (1909). Miers (1876a) distinguished *N. rossi* from *N. hirtipes* because Milne Edwards (1840) described the length of the cephalon of that species to be equal to the width. This description is incorrect, however, consistent differences between *N. rossi* and *N. hirtipes* include a medially produced interocular furrow (smoothly convex in *N. hirtipes*), a convex anterior margin to the eye (angled in *N. hirtipes*), a concave ventral margin to the cephalon (convex in *N. hirtipes*) and a slightly more sinuate anterior margin of the basis of pereopod 7 in *N. hirtipes*. Large males of *N. hirtipes* may develop indistinct tubercles on the dorsal surface of pereonite 2, these are not apparent in material identified as *N. rossi*.

Natatolana rossi is also extremely similar to *N. matong*. The development of the interocular and coxal furrows does not reliably separate the two species as suggested by Bruce (1986). The shape of pleonite 4 is, however, consistently different between the two species, *N. rossi* having a more sinuate posterodorsal margin.

Distribution and ecology. New Zealand and southern Pacific Ocean south of New Zealand. In depths to 260 m (Kussakin, 1967). Marsden (1999) has measured the feeding rate, oxygen consumption and effects of aerial exposure for this species, concluding it is a predator/scavenger capable of long periods of fasting.

Natatolana rusteni n.sp.

Figs. 43–44

Type material. HOLOTYPE: ♂, 8 mm, AM P47158. PARATYPES: 576 specimens AM P38672; ♂, ♀, in BMNH, USNM, ZMUC. • Type locality: off Dobroyd Head, Port Jackson, NSW, Australia, 33°48.7'S 151°16.4'E, [baited trap, unknown substrate, probably sediment], 15 m, [S. Keable, D. Townsend, J. Lowry, 3–4 Jul. 1988, Site 30].

Additional material. New South Wales: ♀, ZMUC CRU122, near Solitary Islands, 29°57'S 153°22'E, 50 m, 11 Nov. 1951, Galathea stn 544; series of 224 specimens, AM P47159–47165, Port Jackson, 33°48.3–50.3'S 151°15.2–16.6'E, baited trap, sediments, 8–13 m, S. Keable *et al.*, 1988; series of 254 specimens,

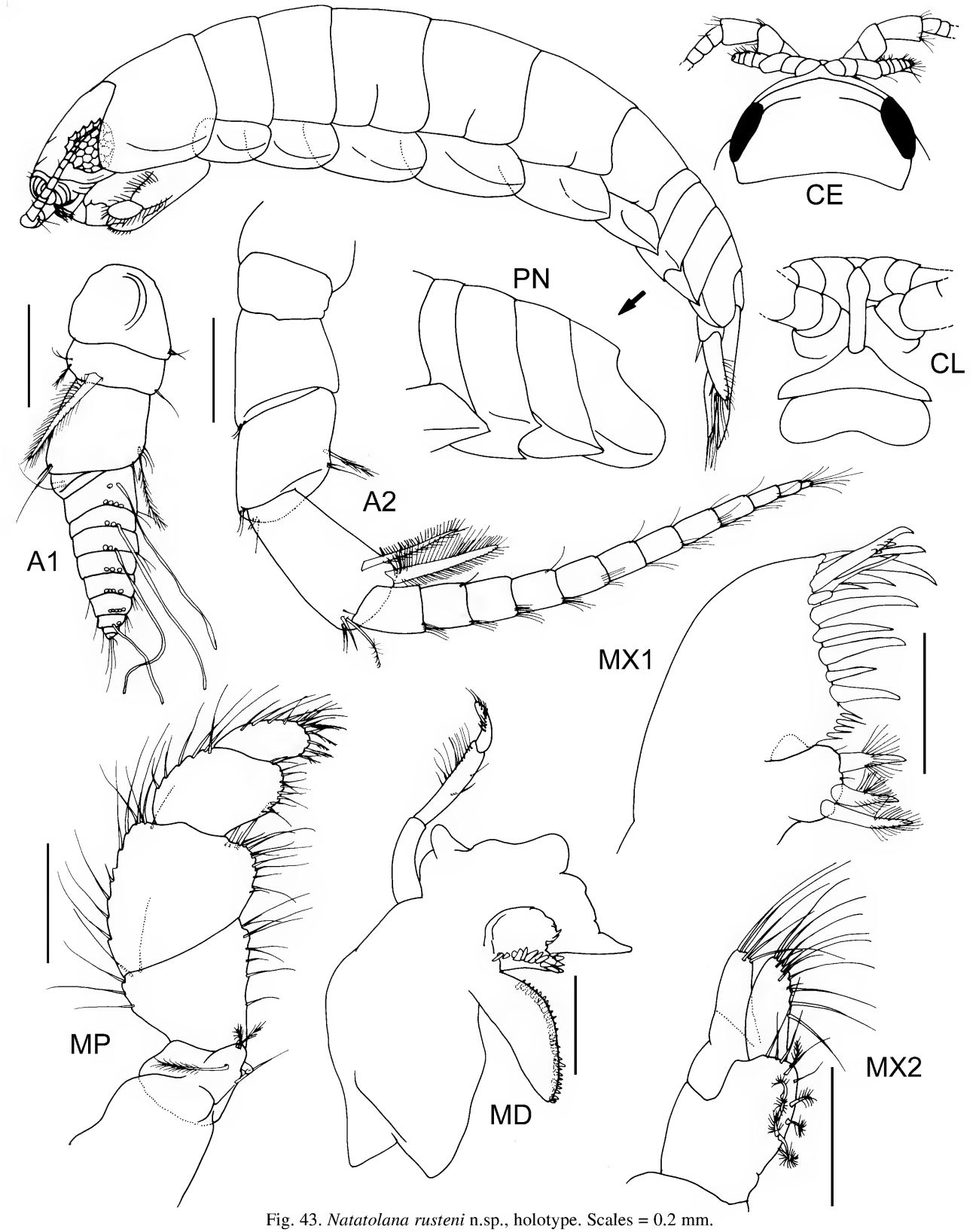

Fig. 43. *Natatolana rusteni* n.sp., holotype. Scales = 0.2 mm.

AM P47166–47172, off Bate Bay/Port Hacking, 34°07.00'S 151°10.00'E, baited trap, sediments, 25–40 m, AM/The Ecology Lab Pty. Ltd. *Pioneer* Consultation Project 1991; series of 18 specimens, AM P47173–47184, Botany Bay, 33°58.25–59.31'S 151°09.91–11.92'S, baited traps, sediments, 5–7 m, S. Keable & R. Springthorpe 1992, AM/Federal Airports Corporation Consultation Project.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.23× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex broadly rounded. *Pleotelson*: narrow, length 1.05× basal width;

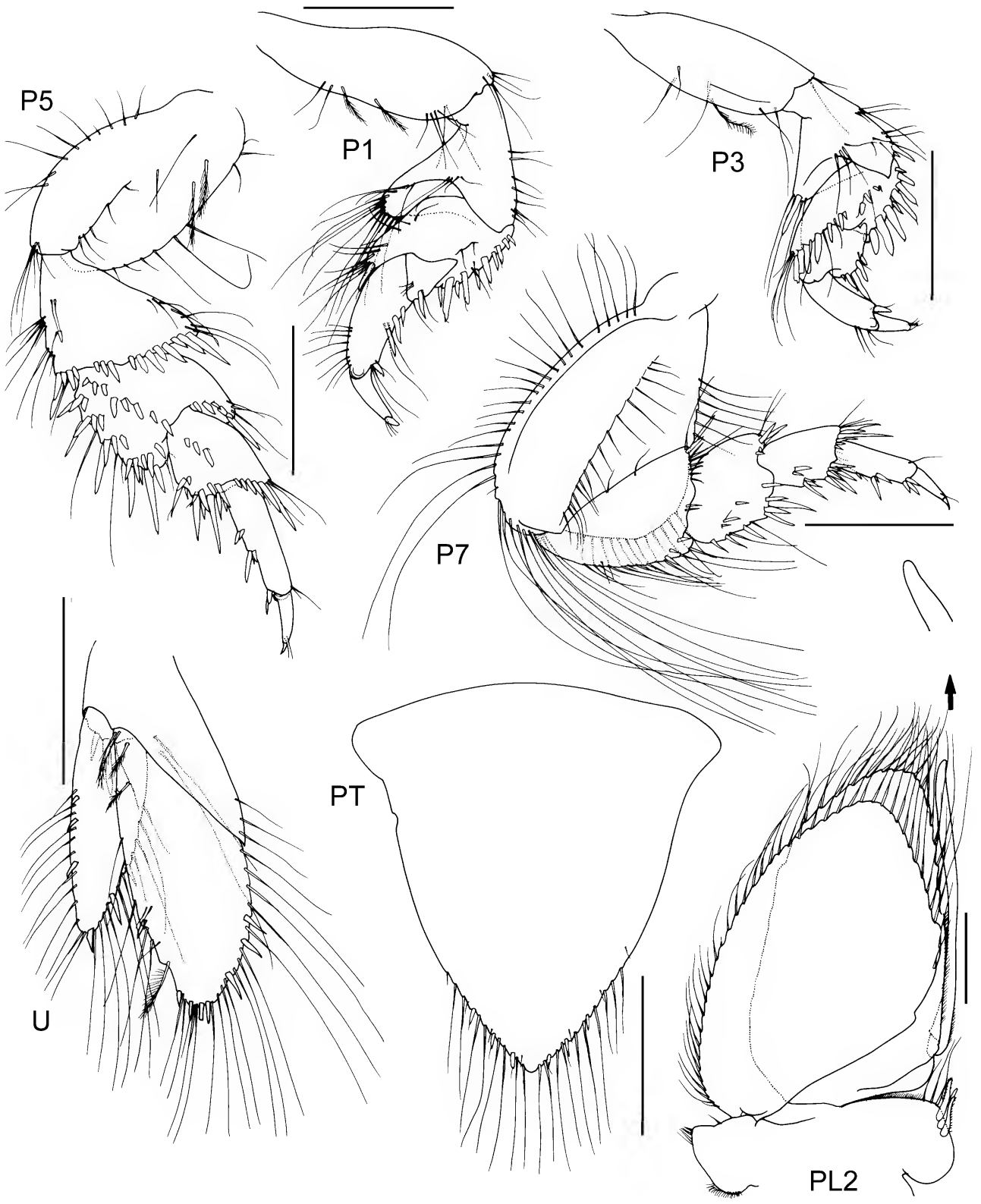

Fig. 44. *Natatolana rusteni* n.sp., holotype. Scales = 0.5 mm, except for MX2 and U = 0.2 mm.

anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 6–7 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.63× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.04× length of endopod; margins very slightly curved laterally; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod short, 0.72× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 3.48× width. Colour cream in alcohol. In freshly preserved material there is often an orange or red/brown colouring on the posterolateral margins of pleonite 4. Chromatophores absent. *Eyes*: with 6 ommatidia in horizontal diameter; with 8 ommatidia in vertical diameter; round; colour red/brown in alcohol. *Frontal lamina*: length c. 5× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 9-articulate. *Antenna*: peduncular article 4 with 1 penicillate seta and 2 SS on posterolateral margin, several PS at anterodistal angle; article 5 with 2 conspicuous pappose setae at posterodistal angle, 1 penicillate seta and 5 SS at anterodistal angle. Flagellum 12-articulate. *Mandible*: setal row with 15 RS. *Maxillule*: medial lobe with 3 large robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 5 SS; medial lobe with 5 SS and 7 PS; middle lobe with 12 SS. *Maxilliped*: endite with 1 coupling hook, and 3 PS. *Pereon*: ornamentation consists of 1 weakly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pereonites 4–6; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: pereonite 1 and coxae 2–5 with rounded posteroventral corners, coxae 6–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin slightly convex; medial carina with PS along entire length; posterior margin convex, PS present. Ischium anterior margin with SS (sparse); posterior margin without RS, PS present. Merus posterior margin with 3 RS (and 3 submarginally), 1 SS. Carpus posterior margin with 3 RS (and 2 submarginally), SS absent. Propodus subequal to carpus; posterior margin with 4 RS, SS absent. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins of pleopods 1–4, only a few setae on pleopod 5. *Uropods*: endopod lanceolate; medial margin convex, with 3 RS, PS along entire length; apex with 3 RS; lateral margin slightly convex, with 2 RS and 1 penicillate seta, PS on distal two-thirds. Exopod medial margin convex, with 2 RS, PS on distal two-thirds; apex acute, with 2 RS (1 missing on side illustrated but socket present and setae present on other side); lateral margin convex, with 3 RS, PS on distal two thirds.

Variation. One paratype specimen has seven robust setae on the pleotelson margin.

Size. Adults to c. 8 mm.

Etymology. Named after Mr Jim Rusten, former storeman at the Australian Museum, in recognition of his help with boats and other field equipment that made collection of the type specimens possible.

Remarks. *Natatolana rusteni* is separated from nearly all other species within the genus by its relatively short antennae that have few flagellar articles. This character, in combination with the number of robust setae on the pleotelson and the shape of the pleotelson, identifies this species as distinct. *Natatolana kahiba* is most similar but has a shorter, less acute pleotelson with four robust setae. *Natatolana lilliput* n.sp. is also extremely similar but also has a shorter, less acute pleotelson and a complete interocular furrow.

Distribution and ecology. Australia: within and off Port Jackson and Botany Bay, and off Solitary Islands, New South Wales. At depths of 5–50 m. Scavenger.

Natatolana sinuosa n.sp.

Figs. 45–47

Cirolana corpulenta.–Hale, 1940: 289 (part) [mis-identification, not *Natatolana corpulenta* (Hale, 1925)].

Natatolana corpulenta.–Bruce 1986: 79, figs. 51–53 (part) [mis-identification, not *Natatolana corpulenta* (Hale, 1925)].

Type material. HOLOTYPE: ♂, 14.5 mm, AM P47214. PARATYPE: ♀, 16.5 mm, TM, same collection data as holotype only 100 m off Pilot Beach, 3 m, TAS-285. • Type locality: between breakwater and Prater Rock, Pilot Bay, Tasmania, Australia, 42°12'S 145°12'E, [baited trap, probably sand bottom], 10 m, [J. Lowry & S. Keable, 26–27 April 1991, TAS-284].

Additional material. **New South Wales**: series from near Newcastle, AM Hunter District Water Board Survey, Shipek [grab] (reported by Bruce [1986]): 1, AM P23034, 1 km east of Belmont Beach, 33°02.36'S 151°41'E, 18 m; 1, AM P23036, 500 m east of Belmont Beach, 33°02.5'S 151°41'E, 14 m; 2, AM P23037, 500 m east of Stockton Beach, 32°54'S 151°47.5'E, 6 m; 2, AM P23038, 1 km east of Stockton Beach, 32°54'S 151°47.5'E, 15 m; 1, AM P23039, 500 m east of Dudley Beach, 32°59'S 151°44'E, 16 m; 37, SAMA C5640, Newcastle, NSW, [32°56'S 151°46'E], from shark liver, T.C. Roughley (reported by Hale [1940]); 156, AM P47221, off Providential Head, 34°44'S 150°39'E, baited trap, 25–30 m, S. Keable & A. Parker 14–15 Jan. 1991, PIO-103. **Tasmania**: series from off Maurouard Beach, St Helens Point, all c. 41°17.3'S 148°21'E, baited trap, J. Lowry, S. Keable & C. McCormick, 13–14 April 1991; 4♂♂, 3♀♀, 31 mancas, AM P47215, sandy bottom, 15 m, TAS-124; ♂, AM P47216, sandy bottom, 5 m, TAS-125; 3♀♀, 23 mancas, AM P47217, sandy bottom, 10 m, TAS-126; 64 mancas, AM P47218, sandy bottom, 15 m, TAS-139; ♀, manca, AM P47219, off Binalong Beach, Binalong Bay, 41°14.7'S 148°17.6'E, baited trap, on sand, 8 m, J. Lowry, S. Keable & C. McCormick, 14–15 April 1991, TAS-144; 21♂♂, 17♀♀, 15 mancas, AM P47220, about 100 m off Nine Mile Beach near Point Bagot, Freycinet Peninsula, 42°06.2'S 148°13.8'E, baited trap, J. Lowry & S. Keable, 30 April–1 May 1991, TAS-344. **South Australia**: ♂, SAMA C5641, Christies Beach [35°08'S 138°28'E], seaweed on beach, T. Castle, 29 Jan. 1959; 6 paratypes of *N. corpulenta*, SAMA C276, Port Willunga [35°16'S 138°28'E].

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins straight, narrowing anteriorly. *Antenna*: c. 0.5× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows moderately developed, on all coxae but indistinct, particularly on coxa 2. Pereonite 1, coxa 2 posterior margins sinuate, posteroventral corners developed into strong coxal points. *Pleonite 4*: posterodorsal margin distinctly concave proximal to meeting posteroventral margin at apex; apex forming a broad acute point. *Pleotelson*: broad, length 0.88× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins concave; apex produced into a large point; with 10 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis narrow, width 0.42× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with

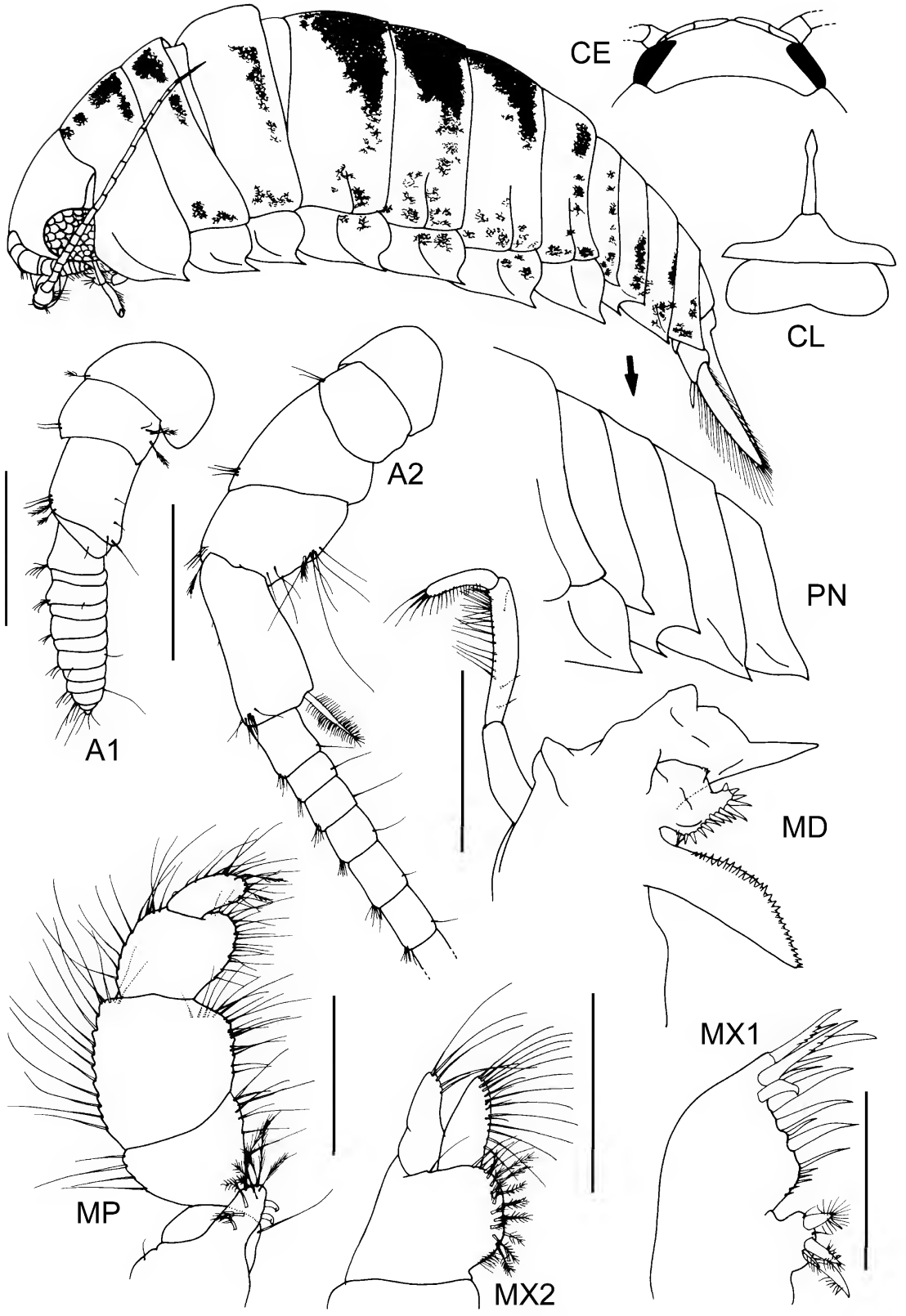

Fig. 45. *Natatolana sinuosa* n.sp., holotype. Scales = 0.5 mm.

setae along entire length. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.07× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.93× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.26× width. Colour yellow in alcohol. Chromatophores present; large; black in alcohol; arranged in bands. *Eyes*: with 7 ommatidia in horizontal diameter; with 7 ommatidia in vertical diameter; round; colour red-brown in alcohol. *Frontal lamina*: length c. 5× basal width;

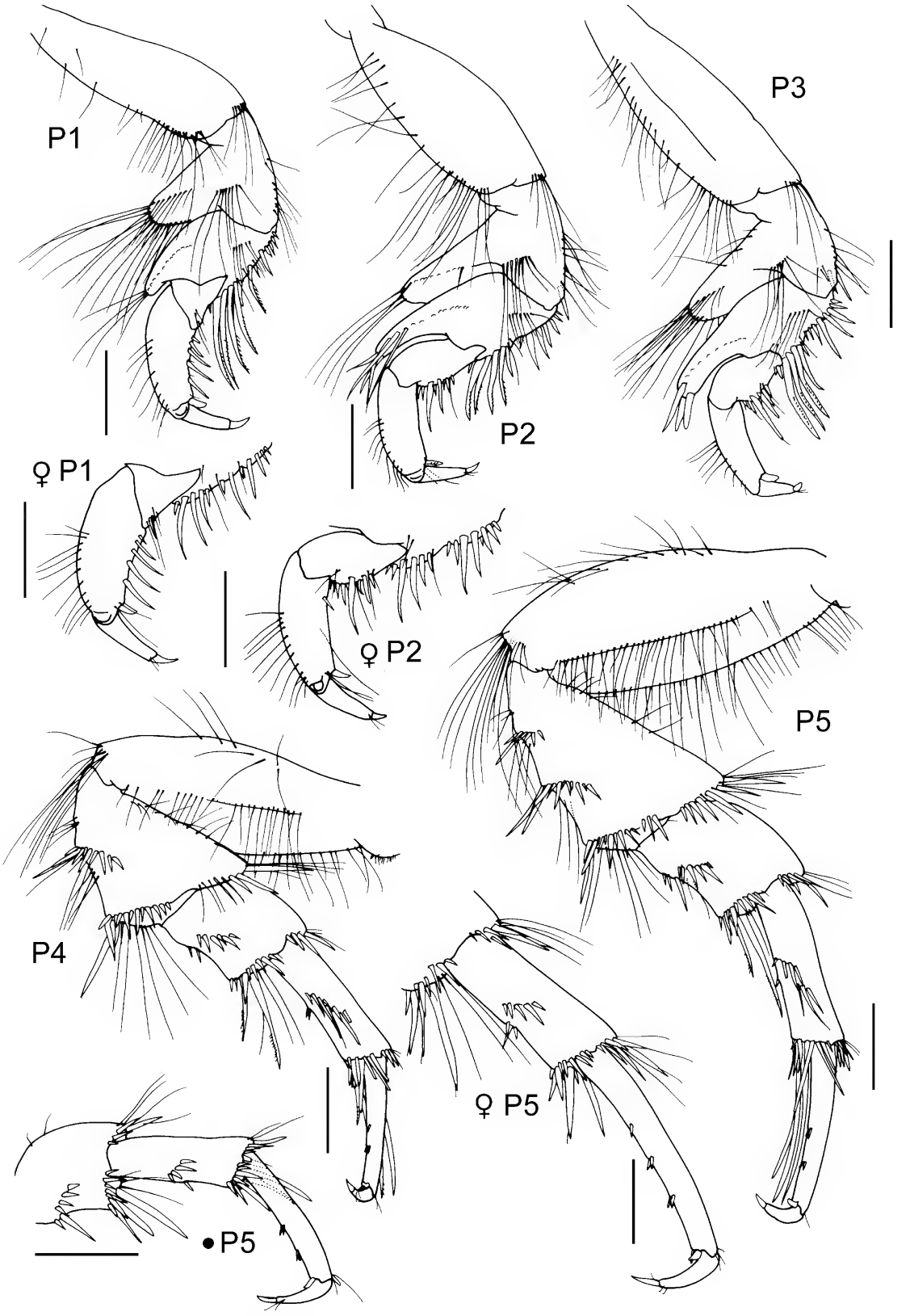

Fig. 46. *Natatolana sinuosa* n.sp., holotype, except; •P5 = male (immature) AM P47215; female = paratype female TM. Scales = 0.5 mm.

apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose and several small penicillate setae; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 12-articulate. *Antenna*: peduncular article 4 with 6 SS and 1 penicillate seta medially and 3 SS at posterodistal angle, 5 SS and 1 penicillate seta at anterodistal angle; article 5 with 1 large pappose seta at posterodistal angle and 8 SS at anterodistal angle. Flagellum 23-articulate. *Mandible*: setal row with 15 RS. *Maxillule*:

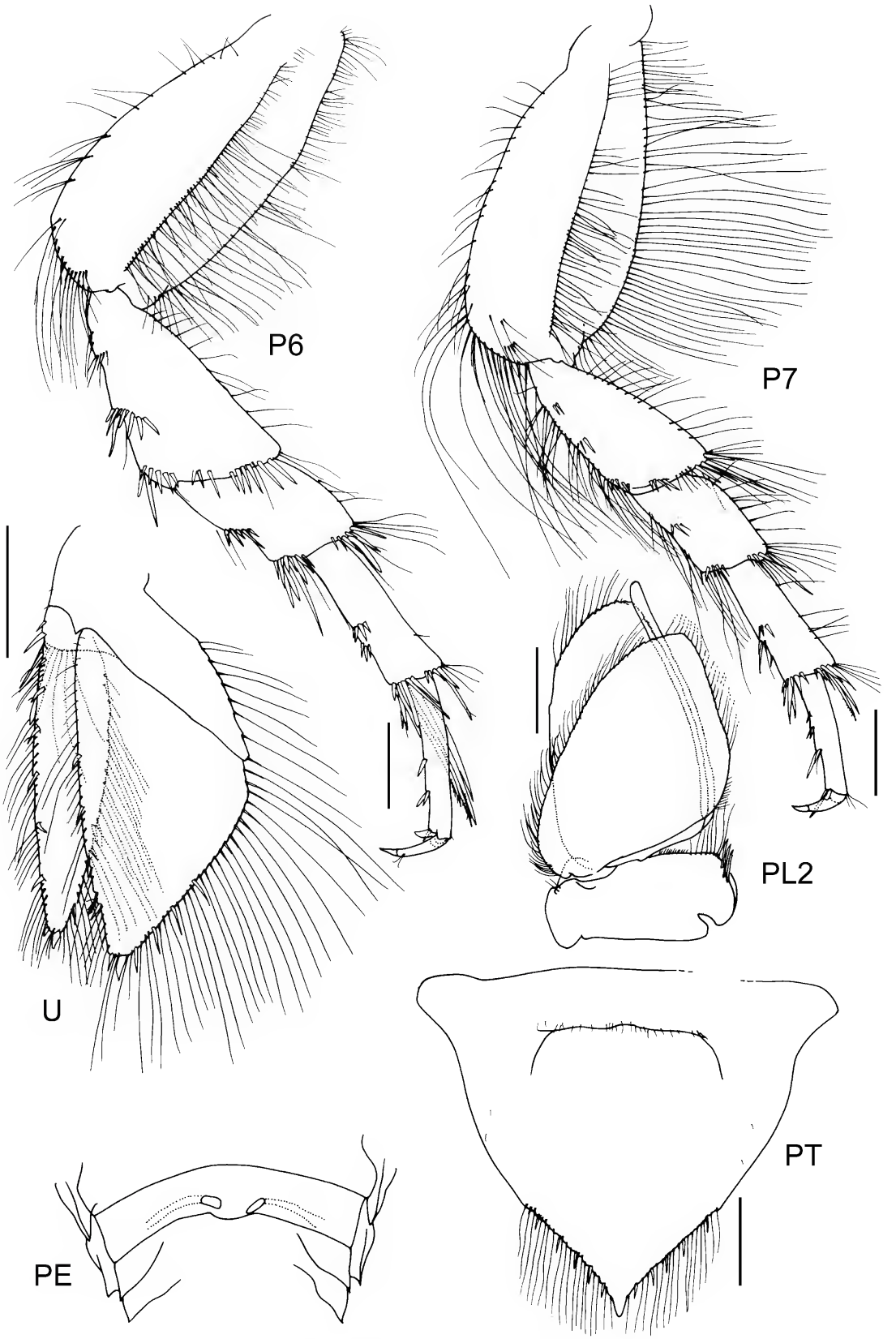

Fig. 47. *Natatolana sinuosa* n.sp., holotype. Scales = 0.5 mm.

medial lobe with 3 large and 1 smaller robust pappose setae and 2 small SS; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 5 SS; medial lobe with 4 SS and 15 PS; middle lobe with 12 long SS on outer row and 7 shorter SS on inner row. *Maxilliped*: endite with 2 coupling hooks, and 9 PS. *Pereon*: ornamentation consists of 1 weakly developed furrow on lateral margin of pereonite 1; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: coxal points strongly developed on posteroventral corners, on all coxae. *Pleonite 2*: dorsal posterolateral margin subequal with ventral

posterolateral margin. *Pereopod 7*: basis anterior margin convex; medial carina with PS and SS present (plumose proximally, mostly slender distally but with a few plumose setae also); posterior margin convex, SS present. Ischium anterior margin with SS; posterior margin with groups of RS present, PS present. Merus anterior margin with SS; posterior margin with 2 RS, SS present. Carpus posterior margin with 6 RS, 1 SS. Propodus subequal to carpus; posterior margin with 6 RS, SS absent. *Penes*: forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod triangular; medial margin slightly convex and obtusely angled proximal to peduncle, with 4 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 4 RS and 1 penicillate seta, PS along entire length. Exopod medial margin convex, with 3 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 6 RS, PS along entire length.

Variation. Small males (to 10.5 mm) are apparently immature and do not have conspicuously elongated robust setae on pereopods 1–6, they also have the appendix masculina shorter than the pleopod endopod. There is also a mixture of specimens both with and without obvious chromatophores in the additional material examined.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Adults to 16.5 mm.

Etymology. From the Latin "sinuosus" (full of windings) in reference to the sinuate posterior margins of the coxae.

Remarks. *Natatolana sinuosa* is most similar to *N. corpulenta*, *N. debrae* n.sp. and *N. femina* n.sp. *Natatolana sinuosa* can be distinguished from these species because it has strongly developed coxal points on the posterolateral margins of pereonite 1 and coxae 2–7. It also lacks an acute tooth at the anteroventral corner of coxa 2 that is found in *N. corpulenta*. *Natatolana longispina* is also very similar but is distinguished from *N. sinuosa* by having less strongly developed coxal points and the pleotelson with convex posterolateral margins.

Distribution and ecology. Australia: New South Wales, east and west coast of Tasmania, and South Australia. Intertidal to 30 m depth.

Natatolana taiti Keable, 1997

Natatolana taiti Keable, 1997: 261, figs. 5–7.–Bruce *et al.*, 2002: 152.

Type material. Holotype: ♂, 8.5 mm, NTM Cr-011524. Paratypes: 12 specimens, AM P44854; 11 specimens, NTM Cr-011516; 11 specimens, BMNH 1995.732-741; 11 specimens, USNM 264080; 11 specimens, ZMUC CRU1714. All examined. • Type locality: between North Shell and South Shell Islands, Darwin Harbour, NT, Australia, 12°29.7'S 130°52.9'E, [baited trap, unknown substrate, probably rocks and muddy sand], 7 m, [S. Keable, 14–15 Jul. 1993, NT-157].

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.3× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: broad, length 0.95× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 4–6 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.53× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal third. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 0.99× length of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod short, 0.79× the length of the endopod.

Variation. The holotype has four robust setae on the pleotelson margins, a subsample of paratype specimens showed 85% have four robust setae, 2% have three, 4% have five and 9% have six. In other material from Shadwell Reef, Queensland, most of the adult specimens have six robust setae on the pleotelson.

Size. Adults to c. 12 mm.

Remarks. *Natatolana taiti* is similar to both *N. woodjonesi* and *N. kahiba*. It differs from adult specimens of these species in having longer antennae, reaching to the posterior of pereonite 3 and 0.3× as long as the body when extended along it (reaching to the posterior of pereonite 2 with 18–21 articles in the flagellum and 0.25× as long as the body in *N. woodjonesi*; reaching to the posterior of pereonite 2, with c. 12–18 articles and 0.25× as long as the body in *N. kahiba*). Other differences include the less acute posterior margins of the pleotelson and uropod endopod apex in *N. taiti*. *Natatolana arrama* and *N. bulba* are also similar to *N. taiti*. Using the key provided by Bruce (1986) these species can only be reached if it is assumed in couplet 21 that they have six or more robust setae on the pleotelson, whereas they only have four, as in *N. taiti*. *Natatolana arrama* differs from *N. taiti* in having a frontal lamina with the apex not expanded; the antennae with c. 18 articles in the flagellum, reaching to the middle of pereonite 2, 0.24× the length of the body; the uropod exopod lateral margin lacking robust setae and the endopod narrower and more lanceolate; and the posterolateral margins of the pleotelson are less convex. *Natatolana bulba* differs in that the uropod endopod is narrower and more lanceolate; the uropod exopod lateral margin lacks robust setae; and the posterolateral margins of the pleotelson are less convex.

Distribution and ecology. Australia: Darwin, Northern Territory; northern Queensland. At depths of 5–35 m. Scavenger.

Natatolana tenuistylis (Miers, 1884)

Cirolana tenuistylis Miers, 1884: 303, pl. 33B.–Hansen, 1890: 356.–Hale, 1925: 136, fig. 4.–Nierstrasz, 1931: 157.–Holdich *et al.*, 1981: 572, fig. 7.–Ellis, 1981: 123.

Natatolana tenuistylis.–Bruce, 1981: 958.–1986: 103, figs. 70, 71.–Keable, 1995: 43.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 152.

Type material. Lectotype designated by Holdich *et al.* (1981): 13.9 mm, BMNH 1882:7 (Bruce (1986) has 1882:1). Paralectotypes: 2, BMNH 1882:53 (Ellis (1981) has 1856:33 for the syntypes). Holdich *et al.* (1981) question the conspecific status of these specimens with the lectotype. Bruce (1986) regards one paralectotype as *Natatolana vieta* and the other as too badly damaged to be identified but most likely to be *N. matong*. None examined. • Type locality: Prince of Wales Channel, Queensland, Australia [10°32'S 142°10'E].

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon (not illustrated by Holdich *et al.* (1981) but present according to Bruce (1986) and in material examined); smoothly convex. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.6× as long as body, reaching to posterior of pereonite 5. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 2*: ventral posterolateral margin acute, formed into long curved process. *Pleonite 4*: apex broadly rounded dorsally, but meeting convex ventral margin at a point. *Pleotelson*: broad, length 0.94× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 8–12 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.6× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal half. *Penes*: absent. *Pleopod 2 appendix masculina*: just shorter than endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, with a distinct acute projection. *Uropods*: exopod slightly shorter than endopod, 0.88× the length of the endopod.

Variation. The lectotype is damaged and has only four robust setae present on one side of the pleotelson apex, Keable (1997) discusses the variation in the total number of robust setae occurring on the pleotelson.

Size. Adults to c. 17.5 mm.

Remarks. Characters that are particularly useful for identifying *Natatolana tenuistylis* are: the complete interocular furrow; the ventral posterolateral margin of pleonite 2 (produced and formed into an acute process); the acute projection on the apex of the appendix masculina; the long antennae, reaching to the posterior of pereonite 5 (c. 0.6× the length of the body); and the unusual shape of the posterolateral margin of pleonite 4 (rounded dorsally and meeting the ventral margin at a point) (Bruce, 1986; Keable, 1997).

Distribution and ecology. Australia: northern Western Australia, Northern Territory, northern Queensland. Papua New Guinea: Daru. At depths of 3–62 m. Scavenger.

Natatolana thalme Bruce, 1986

Natatolana thalme Bruce, 1986: 113, figs. 79, 80.–Springthorpe & Lowry, 1994: 62.–Keable, 1995: 43.–Brusca *et al.*, 1995: 82.–Keable, 1997: 268.–Bruce *et al.*, 2002: 153.

Type material. Holotype: ♂, QM W6292 (not examined). Paratypes: QM W6288, W6291–6293, W9848–9852 (not examined); AM P32382 (examined). • Type locality: Middle Banks, Moreton Bay, Queensland, Australia, 27°06'S 153°16'E.

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.34× as long as body, reaching to posterior of pereonite 3 (not pereonite 2 as described by Bruce [1986]). *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex rounded. *Pleotelson*: narrow, length 1.05× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an acute angle or convex; apex produced into a small point; with 4–6 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth, width 0.49–0.52× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with sparse setae along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, with a distinct acute projection. *Uropods*: exopod slightly shorter than endopod, 0.84× the length of the endopod.

Variation. Type material of *Natatolana thalme* has four robust setae on the margins of the pleotelson, Keable (1997) reported that this was the most common number of robust setae but that some specimens may have six.

Sexual dimorphism. Bruce (1986) reported that males have fewer robust setae on the pereopods than females. This may reflect the difference in size of the material examined.

Size. Males to c. 6.9 mm, females to c. 9.5 mm, mancas to c. 6.0 mm (Bruce, 1986).

Remarks. *Natatolana thalme* is most similar to *N. gallica*. It differs most noticeably from that species in having the posterolateral margins of the pleotelson noticeably angled to the anterolateral margins (convex and smoothly continuous with the anterolateral margins in *N. gallica*), incomplete coxal furrows, sparse setae along the length of the posterior margin of the basis of pereopod 7 (dense in *N. gallica*) and in lacking robust setae on the palm of the propodus of pereopods 2 and 3 (often present in *N. gallica*).

Distribution and ecology. Australia: northern Western Australia, Northern Territory, northern Queensland south to Moreton Bay. Intertidal to 83 m depth. Scavenger.

Natatolana thurar Bruce, 1986

Natatolana thurar Bruce, 1986: 97, figs. 64, 65.–Springthorpe & Lowry, 1994: 62.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 153.

Type material. Holotype: ♀, 15.8 mm, AM P32171. Paratypes: AM P30350. All examined. • Type locality: 10 km southeast of Lakes Entrance, Victoria, Australia, 30°35'S 149°06'E, 149 m [originally cited as Eastern Bass Strait, Australia, 38°35'S 149°06'E, corrected by Springthorpe & Lowry (1994)].

Material examined. **New South Wales**: 8♂♂, 4♀♀, manca, AM P47269, east of Coffs Harbour, 30°14.63'S 153°27.68'E, 199 m, 12–13 Aug. 1993, SEAS NSW-883.

Diagnosis. *Eyes*: vestigial. *Interocular furrow*: well developed, forming a ridge that runs across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.35× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed, coxae 2, 3

and 7 with complete furrows, furrows absent on coxae 4–6. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point. *Pleotelson*: broad, length 0.76× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle or convex; apex not produced, lateral margins converging smoothly to a point; with 8–10 RS. *Pereopod 2*: propodus with 2 RS on palm. *Pereopod 3*: propodus with 2 RS on palm. *Pereopod 7*: basis narrow, width 0.44× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae on proximal quarter. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.93× the length of the endopod.

Variation. This species was originally described as having eight robust setae on the pleotelson. In the material examined from Coffs Harbour there were specimens with either eight or 10 robust setae on the pleotelson.

Size. 12.6–32 mm.

Remarks. This is the first record of a male specimen of *Natatolana thurar*. This species is best identified using the characters discussed under remarks for *N. aotearoa*.

Distribution and ecology. Australia: off Coffs Harbour, New South Wales; off eastern Victoria. At depths of 149–200 m. Scavenger.

Natatolana valida (Hale, 1940)

Cirolana valida Hale, 1940: 290, fig. 2.–Springthorpe & Lowry, 1994: 64.

Natatolana valida.–Bruce, 1981: 958.–1986: 89, fig. 60.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 153.

Type material. Holotype: ♀, 31.0 mm, AM E4814 (examined). • Type locality: east of Flinders Island, Bass Strait [Springthorpe & Lowry (1994) give c. 40°S 148°30'E, 366–549 m].

Material examined. **New South Wales**: 76 including numerous ♂♂ (2 dissected), AM P44412, off Wollongong, 34°33.01'S 151°16.54'E, 400 m, 7–8 May 1993, SEAS NSW-803. **Western Australia**: 6♀♀, NTM Cr 007337, NW of Shark Bay, 26°28'S 112°31'E, pot caught, 400 m, CSIRO Fisheries, 28 April 1990.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: well developed, extending across the cephalon. *Frontal lamina*: lateral margins straight, parallel. *Antenna*: c. 0.4× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows variously developed, coxa 2 and 3 with a strongly developed furrow along ventral margin, coxae 4–7 without furrows. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex forming a narrow acute point, or apex slightly rounded. *Pleotelson*: broad; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline; posterolateral margins straight, markedly angled to anterolateral margins and meeting at an obtuse angle or convex; apex not produced, lateral margins converging smoothly to a point; with 14–20 RS (Hale (1940) records 20 on the holotype but Bruce (1986) notes that some may have rubbed off since the original description and records 16; in the material examined a total of 14 was most common but this ranged up to 20). *Pereopod 2*: propodus with 4 RS on palm. *Pereopod 3*: propodus with 3 RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.91× the length of the endopod.

Variation. In the material from New South Wales (AM P44412) the median downbent process at the anterior of the cephalon is more obvious than in the type specimen. Although Bruce (1986) regarded this process as not constituting the rostral process found in other members of the genus it does appear to be homologous to it. Therefore, the anterior margin of the cephalon is not medially recessed as in other genera, such as *Aatolana* Bruce, 1993.

Size. Adults to c. 40 mm.

Remarks. This is the first record of a male specimen of *Natatolana valida*. This species is most readily recognized by the elongate eyes, lack of penes, morphology of the appendix masculina and frontal lamina with a strongly expanded apex.

Distribution and ecology. Australia: off Shark Bay, Western Australia; off Wollongong, New South Wales; off Flinders Island, Bass Strait. At depths of 400–600 m. Scavenger.

Natatolana variguberna (Holdich, Harrison & Bruce, 1981)

Cirolana variguberna Holdich *et al.*, 1981: 566, fig. 5.–Springthorpe & Lowry, 1994: 64.

Natatolana variguberna.–Bruce, 1981: 958.–1986: 105, fig. 72.–1995a: 409, fig. 19A–E.–Keable, 1995: 43.–Brusca *et al.*, 1995: 82.–Keable, 1997: 269.–Bruce *et al.*, 2002: 153.

Type material. Holotype: ♂, 6.17 mm, QM W6337 (not examined). Paratypes: QM W6338 (not examined); lots of 15, 7 and 207 specimens, institution where deposited not stated, possibly in Nottingham University (not examined); 8, AM P32109–32114, not noted in original description but cited by Springthorpe & Lowry (1994) (examined). • Type locality: Halifax Bay, Queensland, Australia, 19°07'S 146°36'E.

Material examined. Listed by Keable (1997).

Diagnosis. *Interocular furrow*: well developed, extending across the cephalon; smoothly convex. *Frontal lamina*: lateral margins medially constricted, or straight, parallel. *Antenna*: c. 0.4× as long as body, reaching to between the posterior of pereonite 3 to the posterior of pereonite 5. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex forming a broad acute point, or slightly rounded. *Pleotelson*: broad, length 0.7× basal width, anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly toward the midline, or convex (original illustration shows almost straight or concave anterolateral margins, material examined has slightly convex anterolateral margins); posterolateral margins convex; apex produced into a small point; with 4–6 RS. *Pereopod 2*: propodus with 0–1 RS on palm. *Pereopod 3*: propodus without RS on palm. *Pereopod 7*: basis of medium breadth, width 0.5× length; distance between anterior margin and medial carina greater

than between posterior margin and medial carina; posterior margin with setae along entire length or on proximal quarter. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins very slightly curved laterally; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: endopod lateral margin with prominent excision. Exopod short, 0.75× the length of the endopod.

Variation. Type material of this species has six robust setae on the pleotelson margin. Additional material from the type locality and other locations, however, has four robust setae.

Sexual dimorphism. Females may have slightly shorter antennae that extend to the posterior of pereonite 3 whereas in males they extend to the posterior of pereonite 5 (Keable, 1997).

Size. Adults to 10.7 mm (Bruce, 1986) and 11.5 mm (Bruce, 1995a).

Remarks. *Natatolana variguberna* and *N. honu* are the only species of *Natatolana* with a prominent excision near the apex of the uropod endopod lateral margin. *Natatolana variguberna* most noticeably differs from *N. honu* in having well-developed eyes, coxal furrows on all coxae, lacking penes and having fewer robust setae on the pleotelson margins.

Distribution and ecology. Australia: Darwin Harbour and Cobourg Peninsula, Northern Territory; northern Queensland south to Moreton Bay. Papua New Guinea: Madang Lagoon. At depths of 2.7–63 m. Scavenger.

Natatolana vieta (Hale, 1925)

Cirolana vieta Hale, 1925: 150, fig. 11.–1929: 249, fig. 242.–1940: 288, fig. 1.–Nierstrasz, 1931: 157.
Natatolana vieta.–Bruce 1981: 958.–1986: 55 figs. 33, 34.–Jones & Morgan, 1993: 142.–Brusca *et al*., 1995: 82.–Kensley, 2001: 230.–Bruce *et al*., 2002: 153.

Type material. Holotype: ♀, 13 mm, SAMA C278 (examined). • Type locality: Encounter Bay, South Australia, Australia [35°35'S 138°45'E].

Material examined. **Queensland**: 3, AM P47268, off East Fitzroy Reef, 23°32.53'S 152°16.45'E, 105 m, 16–17 Jun. 1993, SEAS QLD-956. **New South Wales**: 2, AM P47267, east of Coffs Harbour, 30°17.49'S 153°13.90'E, 45.4 m, 11–12 Aug. 1993, SEAS NSW-873; series from off Providential Head, c. 34°44'S 150°39'E, baited traps, 25–38 m, S. Keable, A. Parker & J. Lowry on MV Krista, 14–15 Jan. 1991, Australian Museum/The Ecology Lab Pty. Ltd. *Pioneer* Consultation Project 1991: AM P47247–47254. **Tasmania**: 1, AM P47264, east of Fortescue Bay, 43°06.70'S 148°03.45'E, 100 m, 16–17 April 1993, SEAS TAS-354. **South Australia**: series from Upper Spencer Gulf, 32°42.2'–33°5'S 137°47.26'–57.44'E, 5–17 m, Fisheries Department Survey, SAMA C5642–5648. **Western Australia**: series from North-West Shelf, 19°3.5–5.4'S 118°50.8–119°3.1'E, 81–84 m, sled, CSIRO 1983; 5, AM P47259–47263.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins concave but not medially constricted, narrowing toward apex. *Antenna*: c. 0.8–1.05× as long as body, reaching to between pleonite 4 and just beyond the pleotelson. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex acute and slightly produced. *Pleotelson*: narrow, length 0.91× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex produced into a large point; with 4–8 RS. *Pereopod 2*: propodus with 6 RS on palm. *Pereopod 3*: propodus with 5 RS on palm. *Pereopod 7*: basis narrow, width 0.38× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae proximally and distally but not medially. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins moderately curved laterally; apex not at angle to adjacent margins, blunt with a minute spiniform process or bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.85× the length of the endopod.

Variation. Bruce (1986) noted that the scattered furrows, giving a "wrinkled" appearance to the dorsal surfaces of the various body segments that is characteristic of *Natatolana vieta*, tend to be more developed in larger specimens. This is not the case in the material examined, specimens from Upper Spencer Gulf have clearly developed furrows while specimens of a similar size (or larger) from other localities do not have well-developed furrows. Bruce (1986) illustrated a complete interocular furrow for this species. This appears to be formed from the scattered wrinkle like furrows occurring elsewhere on the body and is not apparent in specimens lacking wrinkles.

The specimens from the North-West Shelf of Western Australia have six to eight robust setae on the pleotelson rather than the usual four found in the other material examined. In material with scattered furrows, the geniculate appearance of the antennular peduncle is more strongly developed. In material examined from Queensland and New South Wales, the spiniform process on the apex of the appendix masculina is not developed.

Sexual dimorphism. Females may have shorter antennae (c. 0.8× body length) than males (c. 1.05× body length) (Hale, 1940). This is not, however, a constant feature, some males having the antennae only as long as females.

Size. Females to 27.7 mm, mancas to 8.5 mm.

Remarks. Characters that separate *Natatolana vieta* from all other species, when used in combination, are the long antennae and the presence of a distinct dorsal depression on the pleotelson.

Distribution and ecology. Australia: northwestern Western Australia, south to Rottnest Island; Queensland, north to Gladstone; New South Wales; Victoria; Tasmania; South Australia. At depths of 5–156 m. Scavenger.

Natatolana virilis (Barnard, 1940)

Figs. 48–50

Cirolana virilis Barnard, 1940: 393 fig. 7d.–Kensley, 1975: 39 (part, specimen from SST.101.D).–1978: 72, fig. 29I.–1984: 215.
Natatolana virilis.–Bruce, 1981: 958.–1986: 222.–Brusca *et al*., 1995: 82.–Kensley, 2001: 230.
Not *Cirolana virilis*.–Kensley, 1975: 39 (part, specimen from SST.54.N) [mis-identification = *Natatolana* n.sp.].

Type material. Holotype: ♂, 13.5 mm, SAM-A150997 (examined). • Type locality: Algoa Bay, South Africa, 33°59'S 25°43'E, 60 m.

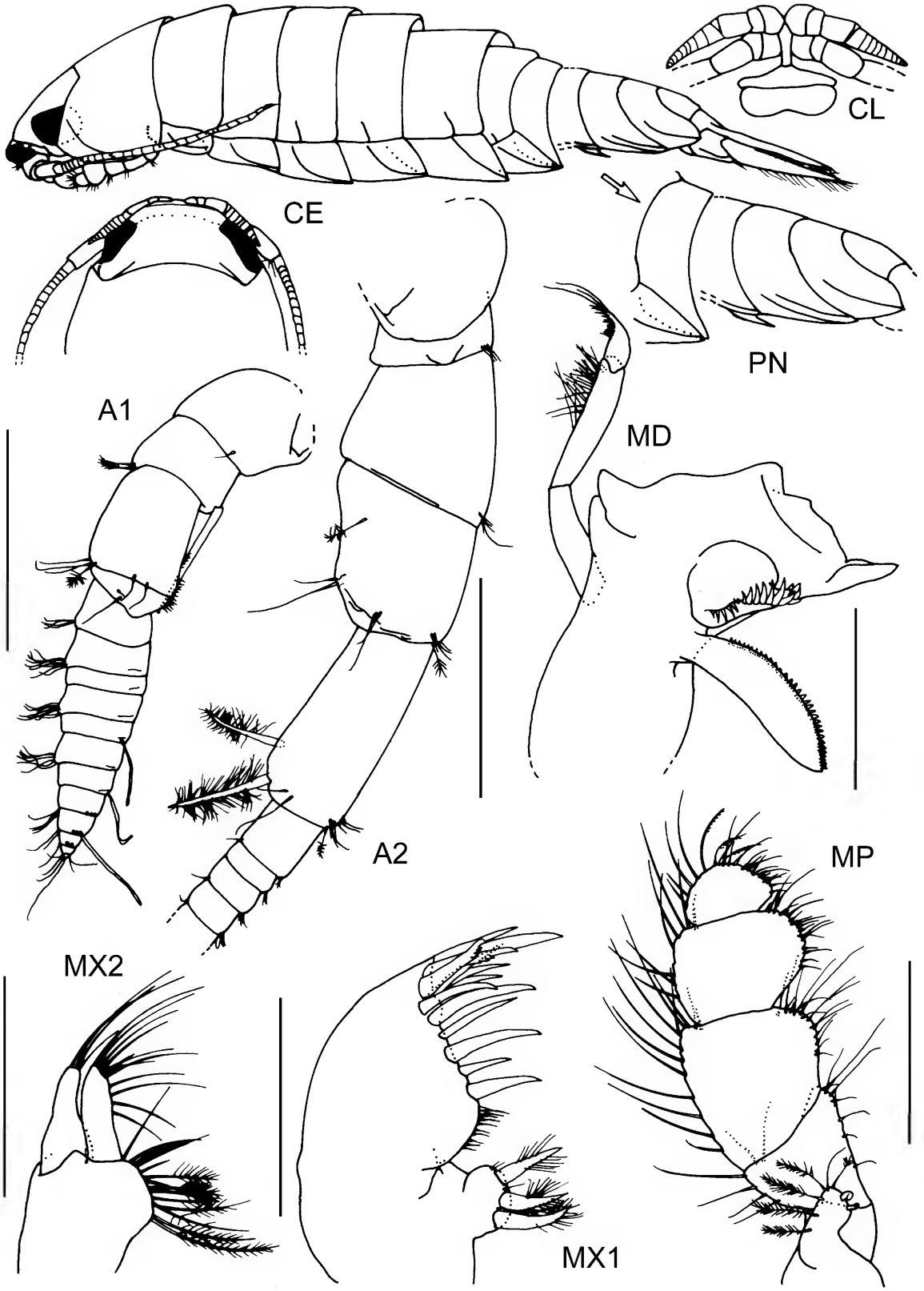

Fig. 48. *Natatolana virilis* holotype male. Scales = 0.5 mm.

Material examined. **South Africa**: ♀, 10.5 mm, SAM A-19334, 31°59.3'S 29°22.5'E, dredge, RV *Meiring Naude*, 150–200 m, 25 Jun. 1979, Sta No:SM 250.

Diagnosis. *Eyes*: well developed; elongate, length c. 2× height. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon (but very faint partial furrow medially). *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4× as long as body, reaching to between the posterior of pereonite 3 and three-quarters of the way along pereonite 4. *Coxal plates*: furrows moderately

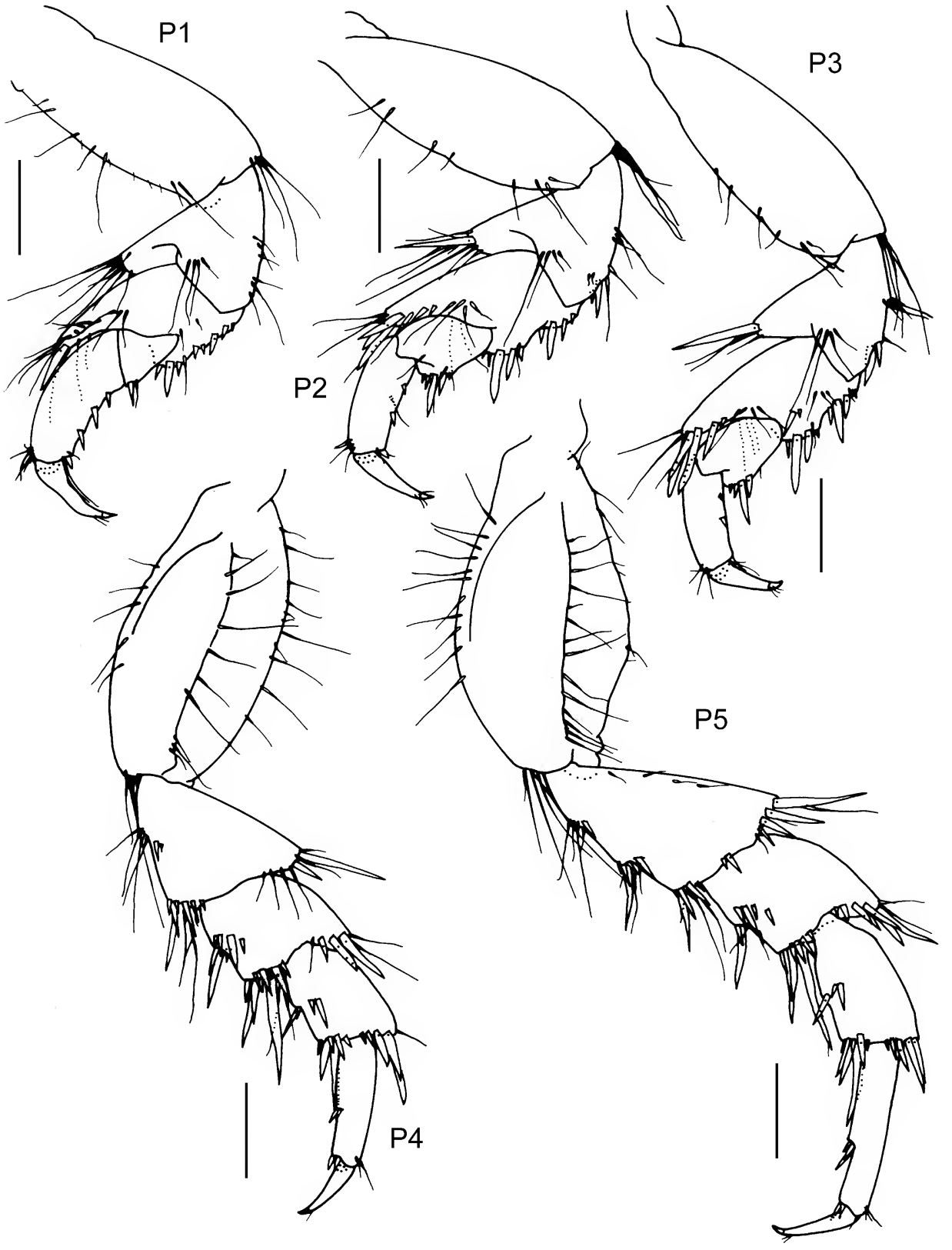

Fig. 49. *Natatolana virilis* holotype male. Scales = 0.5 mm.

developed, on all coxae. *Pleonite 4*: apex forming a broad acute point. *Pleotelson*: broad, length 0.89× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex not produced, lateral margins converging smoothly to a point; with 14–16 RS. *Pereopod 2*: propodus with 1–2 RS on palm. *Pereopod 3*: propodus with 1–2 RS on palm. *Pereopods 5–7*: propodus long, but on pereopod 5 less than 2× the length of that of pereopod 7 (apparently, but uncertain because the distal articles of pereopod 7 are missing in the material examined).

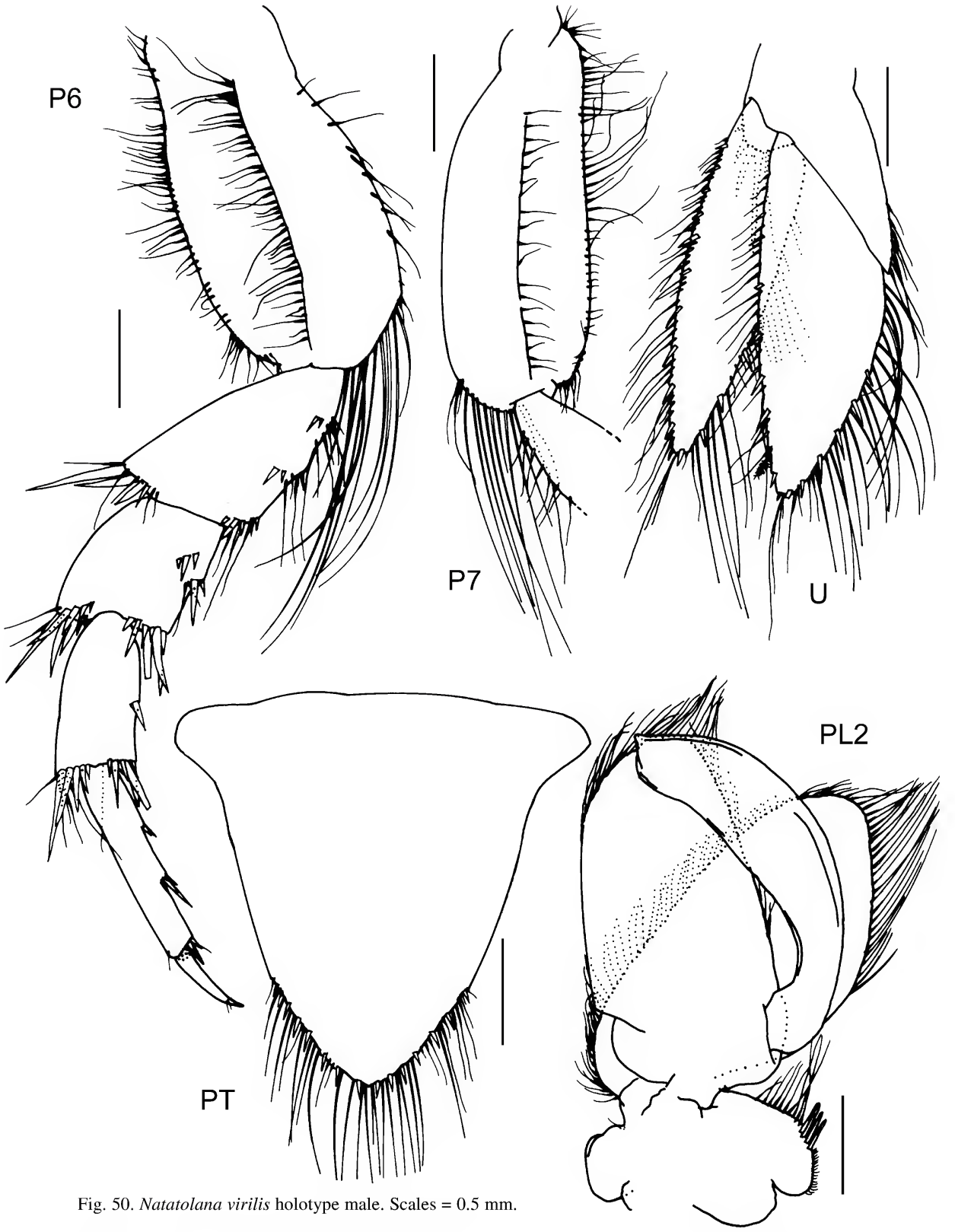

Fig. 50. *Natatolana virilis* holotype male. Scales = 0.5 mm.

Pereopod 7: basis narrow, width 0.37× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with setae completely absent along entire length. *Penes*: absent. *Pleopod 2 appendix masculina*: extending subequal with tip of endopod, 1.03× length of endopod; margins very strongly curved laterally; broad; apex not at angle to adjacent margins, truncate. *Uropods*: exopod subequal to endopod, 0.93× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 3× width. Colour cream to white in alcohol. Chromatophores absent. *Eyes*: with c. 16 ommatidia in horizontal diameter; with c. 9 ommatidia in vertical

diameter; narrower anteriorly; colour burgundy red in alcohol. *Frontal lamina*: length c. 4× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 12-articulate. *Antenna*: peduncular article 4 with 1 penicillate seta medially on posterolateral margin, 2 SS at posterodistal angle, 2 penicillate setae and 1 SS at anterodistal angle; article 5 with 2 large pappose setae at posterodistal angle. Flagellum 29-articulate. *Mandible*: setal row with 17 RS. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae; lateral lobe with 13 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 6 SS and 8 PS; middle lobe with 12 SS. *Maxilliped*: endite with 2 coupling hooks, and 6 PS. *Pereon*: ornamentation consists of 1 weakly developed furrow on lateral margins of pereonites 1 and 4–7; pereonites 1 and 6 subequal in length and longest, 2–5 subequal and longer than 7. *Coxae*: pleonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin straight; medial carina with SS; posterior margin convex. Ischium damaged and other distal articles missing. *Pleopod 2 appendix masculina*: arising sub-basally. *Pleopod 5*: exopod suture strongly developed; only a few endopod PS present. *Uropods*: endopod lanceolate; medial margin convex, with 5 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 5 RS and 1 penicillate seta, PS along entire length. Exopod medial margin convex, with 4 RS, PS along entire length; apex acute, with 2 RS; lateral margin straight, with 10 RS, PS along entire length.

Size. Adults to 13.5 mm (Barnard, 1940; Kensley, 1978).

Remarks. Barnard (1940) stated that he only had a single male specimen of *Natatolana virilis* (i.e., the holotype). The material described here is registered as the holotype but this status is questionable because of differences to the original description and because of the presence of body parts from more than one individual as noted below. In this material a previous dissection has separated pleonites 2–5, the pleotelson and uropods from the rest of the body, pleopods 1–5 have also been removed from the left side and pleopods 1–3 (and part of pleopod 4) from the right side. Pereopods 1 and 7 from the left side and pereopod 6 from the right side have also been previously removed. Both the dissected pereopod 7 and that still attached to the body are incomplete. There is also an additional pereopod 6 or 7 from a larger specimen and a single pleopod 2 that has the appendix masculina straight and slender, not very stout and strongly curved as described and illustrated by Barnard (1940). These additional parts have not been used in the redescription of the species.

The body in the type material matches the brief description of Barnard (1940) reasonably well, although he described the interocular furrow as confined to the hind margins of the eyes and not continuous across the median area. A faint discontinuous furrow can, however, be traced between the eyes. Barnard also indicated that the pleotelson has 16 robust setae but in this material there are only 14 and no sockets to indicate there may have been more.

Among the parts that appear to have been dissected from the apparent holotype, there is a pair of second pleopods with appendix masculina that match the original description and illustration perfectly. This distinguishes *N. virilis* from all other species of *Natatolana*. Unfortunately, because these pleopods cannot be conclusively linked with the material with which they are registered, some doubt must remain as to the validity of the parts described here as type material. No further male specimens identified as *N. virilis* are available in SAM collections to help resolve this question. A female specimen examined (SAM A-19334), however, matches the assumed type material in diagnostic features other than the sexual characters. This indicates that the parts identified as type material are unlikely to have been mixed together from more than one species or individual.

A female specimen from off Still Bay (Kensley, 1975; SAM A-14593) was also examined. This specimen is similar to the material identified here as *Natatolana virilis* but has sinuate, rather than straight, posterior margins on coxae 3–6 with their posteroventral margins formed into notched coxal points rather than being rounded or broadly acute. The antennae of this specimen reach to the posterior of pereonite 5 rather than to the anterior of pereonite 4 as described by Barnard (1940) and also found in the other material examined in this study. This specimen is from a new species but the material is inadequate to describe.

Distribution. South Africa: Port Elizabeth to Natal. At depths of 60–200 m (Barnard, 1940; Kensley, 1975, 1978; Bruce, 1986; this study).

Natatolana woodjonesi (Hale, 1924)

Cirolana woodjonesi Hale, 1924: 71, fig. 2, pl. 2.–1925: 137, fig. 5 (part).–1929: 248, figs. 232, 233, 240.–Nierstrasz, 1931: 157.–Naylor, 1966: 184.–Poore *et al.*, 1975: 33.–Holdich *et al.*, 1981: 575, fig. 9.

Cirolana woodjonsoni.–Roman, 1970: 167, 192, 195, 197 [*lapsus*].

Natatolana woodjonesi.–Bruce, 1981: 958, figs. 1d–e, 2c–d, 3e–f, 4c, 5c–d.–1986: 98, figs. 66, 68.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 154.

Not *Cirolana woodjonesi*.–Hale, 1940: 288 [mis-identification = *Natatolana bulba* Bruce, 1986; *Natatolana arcicauda* (Holdich, Harrison & Bruce, 1981)].

Type material. Hale (1924) did not designate type specimens, instead the description "is based upon a series taken from body cavity of a Port Jackson shark... collected by Mr Collyer". Specimens from several other locations and variation within the species were also mentioned in the original description. Therefore, there was originally a syntype series and all the material initially mentioned by Hale (1924) is accordingly registered as syntypes in the SAMA: 3 specimens, C230, Beachport, South Australia, 3–4 fm, H.M. Hale (examined, re-identified as *N. wowine* Bruce, 1986); 21 specimens, C231, Elliston, Eyre Peninsula, South Australia, on bait when line fishing, H.M. Hale (examined, re-identified as *N. wowine* Bruce, 1986); ♂, C228, Gulf St. Vincent, from body cavity of *Heterodontus phillipi* (Port Jackson shark), H. Collyer (examined); 36 specimens, C160, Gulf St. Vincent, from body cavity of *Heterodontus phillipi* (Port Jackson shark), H. Collyer (examined). Hale (1925) illustrated a "type male" and gave Gulf St. Vincent as "type loc.". Under ICZN article 74.5 this qualifies as a lectotype designation. Unfortunately, Hale did not clearly indicate which specimen from the Gulf St. Vincent material this male was. Holdich *et al.* (1981)

recognized a male specimen (SAMA C228), previously noted by Hale (1924) as the largest specimen, as the "Type" and St. Vincent Gulf as the type locality. Bruce (1986) under the heading material examined noted "Holotype, male" and under the heading "Types" noted "Held by the South Australian Museum, Adelaide, C228", it was also stated that the type locality is Port Willunga, South Australia. The male C228, however, should be regarded as a lectotype, the other material registered as syntypes are paralectotypes and the exact type locality is not known more precisely than Gulf St. Vincent, South Australia. • Type locality: Gulf St. Vincent, South Australia, [Australia].

Material examined. **New South Wales**: 195, AM P38676, off Grotto Point, Port Jackson, 33°49.2'S 151°15.75'E, baited trap, unknown substrate, probably sediment, 10 m, S. Keable, J. Lowry & D. Townsend, 16–17 Jul. 1988. **Tasmania**: 169, AM P47246, about 1 km off steps at south end of Ocean Beach on a line towards Cape Sorell Lighthouse, 42°09.4'S 145°15'E, baited trap, sand, 16 m, J. Lowry & S. Keable, 27–28 April 1991, TAS-305.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.26× as long as body, reaching to posterior of pereonite 2. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad or narrow, length 0.96–1.01× basal width; anterodorsal depression absent; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 3–6 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.7–0.8× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae along entire length. *Penes*: absent, vasa deferentia opening flush to surface of sternite 7 (although Bruce (1986) indicates the penes to be present as small papillae). *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.04–1.06× length of endopod; margins very slightly curved laterally or straight; slender; apex recurved, bent slightly medially, bluntly rounded. *Uropods*: exopod slightly shorter than endopod, 0.84–0.87× the length of the endopod.

Variation. Pleotelson and uropod robust setal counts from margins (n=10), paralectotypes SAMA C160: Pleotelson: 2:2 (100%). Endopod, medial: 3 (10%), 4 (90%); lateral: 2 (90%), 3 (10%). Exopod, medial: 1 (10%), 2 (90%); lateral: 4 (60%), 5 (40%). Pleotelson and uropod robust setal counts from margins (n=10), non type material AM P38676. Pleotelson: 2:1 (10%), 2:2 (50%), 2:3 (10%), 3:3 (30%). Endopod, medial: 4 (90%), 5 (10%); lateral: 2 (100%). Exopod, medial: 2 (100%); lateral: 5 (100%). Specimens from Port Jackson (AM P38676) have a narrower pleotelson than the type material.

Sexual dimorphism. Females may be larger than males.

Size. Largest female 19.9 mm.

Remarks. Hale (1924) mentions variation in the number of articles present in the antennal flagellum of *Natatolana woodjonesi*. This is probably because there are two species in the original syntype series. The specimens from Beachport (SAMA C230) and those from Elliston (SAMA C231) appear to be *N. wowine*, a species that has longer a antennal flagellum containing more articles than are found in *N. woodjonesi*. In *Natatolana woodjonesi* the antenna reach to the posterior of pereonite 2 and there are up to c. 21 articles in the flagella. In *N. wowine* the antenna extend to the posterior or pereonite 3 and the flagella contain up to c. 28 articles.

Figures of the lectotype of *Natatolana woodjonesi* in Holdich *et al.* (1981) have two omissions. The uropod exopod is shown and described as having two robust setae on the lateral margin. There are actually four to five robust setae on this margin, some of which are flattened and difficult to see. The illustration of pereopod 7 lacks the slender setae along the anterior margin of the ischium as shown by Hale (1924), Hale (1925) and Bruce (1986).

Distribution and ecology. Australia: New South Wales, Victoria, Tasmania, South Australia. In depths to 82 m. Scavenger.

Natatolana wowine Bruce, 1986

Natatolana wowine Bruce, 1986: 118, figs. 81, 82.–Hutchings *et al.*, 1993: 13.–Springthorpe & Lowry, 1994: 65.–Brusca *et al.*, 1995: 82.–Bruce *et al.*, 2002: 154.

Cirolana woodjonesi.–Hale, 1924: 71–72 (part).–1925: 137 (part) [mis-identification, not *Natatolana woodjonesi* (Hale, 1924)].

Type material. Holotype: ♂, NMV J1723 (not examined). Paratypes: NMV J1724–1731 (not examined); AM P9592, P9594, P32366–32370 (examined); WAM 18–80 (examined). • Type locality: Crib Point, Western Port, Victoria, Australia, 8°23'S 145°14'E.

Material examined. **Queensland**: series from due east of Mooloolaba, 26°35.42'S 153°41.50'E, 206 m, 2–4 Aug. 1994: ♀, AM P47606, SEAS QLD-1128; 2♀♀, AM P47607, SEAS QLD-1148. **New South Wales**: series from northeast and north of Coffs Harbour, 11–13 Aug. 1993; ♂, AM P47608, 30°15.86'S 153°21.90'E, 92.7 m, SEAS NSW-870; ♂, AM P47609, 30°14.63'S 153°27.68'E, 199 m, SEAS NSW-883; ♀, AM P47610, 30°14.84'S 153°27.69'E, 182.9 m, SEAS NSW-867; series from off Wollongong: 35, AM P47611, 34°32.02'S 151°13.00'E, 200 m, 6–7 May 1993, SEAS NSW-780; 52, AM P47612, 34°32.53'S 151°17.07'E, 400 m, 6–7 May 1993, SEAS NSW-787. **Victoria**: 95, AM P47613, southeast of Bastion Point, Mallacoota, 37°36.6'S 149°48.3'E, baited trap, ?bottom, 30 m, J. Lowry & S. Keable, 29–30 Nov. 1988, NSW-398. **Tasmania**: many, AM P47614, 100 m off south side Esperance Point, Port Esperance, 43°19.8'S 147°3.8'E, baited trap, ?bottom, 24 m, J. Lowry & S. Keable, 19–20 April 1991, TAS-205; 12, AM P47615, mouth of Fortescue Bay, 43°07.77'S 145°59.47'E, 50 m, 17–18 April 1993, SEAS TAS-368. **South Australia**: 3 paralectotypes of *Natatolana woodjonesi*, SAMA C230, Beachport; 21 paralectotypes of *Natatolana woodjonesi*, SAMA C231, Elliston, Eyre Peninsula; series from Upper Spencer Gulf: SAMA C5617–5639, 32°–33°5'S 137°37.38–57.4'E, 7–22 m, South Australia Fisheries Department Survey, Feb. 1987.

Diagnosis. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.39× as long as body, reaching to posterior of pereonite 3. *Coxal plates*: furrows moderately developed, on all coxae. *Pleonite 4*: apex broadly rounded. *Pleotelson*: broad, length 0.77–0.92× basal width; anterodorsal depression absent; anterolateral margins almost straight and angling posteriorly

toward the midline, or convex; posterolateral margins convex or broadly rounded; apex not produced, lateral margins converging smoothly to a point; with 6–8 RS. *Pereopods 2–3*: propodus without RS on palm. *Pereopod 7*: basis broad, width 0.64× length; distance between anterior margin and medial carina greater than between posterior margin and medial carina; posterior margin with setae on proximal two-thirds. *Penes*: absent. *Pleopod 2 appendix masculina*: extending beyond tip of endopod; margins very slightly curved laterally; slender; apex recurved, bent slightly medially, acute. *Uropods*: exopod slightly shorter than endopod, 0.87× the length of the endopod; lateral margin with or without RS.

Variation. Bruce (1986) recorded a variation in the "roundness of the pleotelson," i.e., the posterolateral margins of the pleotelson may be convex converging smoothly to a point or broadly rounded. Bruce (1986) also recorded variation in the number of robust setae on the margins of the pleotelson, from seven or eight in material from Victoria, to six in specimens from Tasmania and Western Australia. In the material examined here in samples from New South Wales (Coffs Harbour: AM P47608, AM P47609; Wollongong: AM P47611, AM P47612) and eastern Tasmania (AM P47614, AM P47615), specimens had both six and eight robust setae on the pleotelson margins. The most common number of robust setae on the pleotelson margins was six, in all samples, except for AM P47615 (eastern Tasmania) where 10 specimens had eight and only two had six. Variation was also found in the number of robust setae on the lateral margins of the uropod exopod, ranging from none to five but most commonly five. All of the material from the South Australia Fisheries Department Upper Spencer Gulf Survey lack robust setae on the uropod exopod lateral margin, as do specimens from eastern Victoria (AM P47613). Most of the specimens in AM P47614 (eastern Tasmania) also lack these setae although they are present on five specimens from this sample. Examination of the paratypes in AM P9592 (17 specimens, not two as recorded by Springthorpe & Lowry [1994]) and P9594 (18 specimens) (material recorded by Hale (1925) as "Tasmania: off Cape Portland" and "New South Wales: 'From porpoise'", respectively) shows that they also lack robust setae on the uropod exopod lateral margin.

Sexual dimorphism. Females tend to be larger than males and ovigerous females may be slightly broader.

Size. Adults to 35 mm (Bruce (1986) records largest male 19.0 mm, largest female 17.6 mm), largest manca to c. 8 mm.

Remarks. Examination of the paralectotypes of *Natatolana woodjonesi* show that they include specimens of *N. wowine*. The falcate apex of the appendix masculina of specimens of *N. wowine* is distinctive. This combined with details of the frontal lamina, length of the antennae, pleonite 4, pleotelson and uropods are the most useful features in separating this species from similar species.

Distribution and ecology. Australia: southern Queensland; New South Wales; Tasmania; Mallacoota, Western Port, Port Phillip Bay, in Victoria; Upper Spencer Gulf, Beachport, Elliston, Eyre Peninsula, in South Australia; Recherche Archipelago, in Western Australia. At depths of 6–400 m. Scavenger.

Natatolana zebra n.sp.

Figs. 51–53

Type material. HOLOTYPE: ♂, 11 mm, AM P47225. PARATYPES: 562 specimens, AM P47226; ♀, AM P47227; subadult ♂, AM P47228; ♂, ♀, TM, BMNH, USNM, ZMUC. • Type locality: about 25 m off middle of breakwater, Pilot Bay, Tasmania, Australia, 42°12.4'S 145°12.4'E, [baited trap, unknown substrate, probably sand], 6 m, [J. Lowry & S. Keable, 26–27 April 1991, TAS-286].

Additional material. **Tasmania**: 2, AM P47229, about 250 m offshore, and just to the east of Hannants Bight on a line toward large bluff of Ocean Beach north side of Cape Sorell, 42°11.5'S 145°11.4'E, baited trap, sand, 25 m, J. Lowry & S. Keable, 26–27 April 1991, TAS-282; 16, AM P47230, between breakwater and Prater Rock, Pilot Bay, 42°12'S 145°12'E, baited trap, probably sand bottom, 10 m, J. Lowry & S. Keable, 26–27 April 1991, TAS-284; 59, AM P47231, same data as holotype, except 100 m off Pilot Beach, 3 m, TAS-285.

Diagnosis. *Interocular furrow*: absent. *Frontal lamina*: lateral margins medially constricted. *Antenna*: c. 0.4× as long as body, reaching to posterior of pereonite 4. *Coxal plates*: furrows strongly developed, on all coxae. *Pleonite 4*: apex slightly rounded. *Pleotelson*: broad, length 0.95× basal width; anterodorsal depression present; anterolateral margins convex; posterolateral margins convex; apex produced into a small point; with 10 RS. *Pereopods 1–6*: males with conspicuous elongated RS subequal to propodus on the merus of pereopods 1–3 and extending from the carpus to dactylus of pereopods 4–6. *Pereopods 2–3*: propodus without RS on palm. *Pereopods 5–7*: propodus long, on pereopod 5 greatly elongate, 2× that of pereopod 7. *Pereopod 7*: basis narrow, width 0.35× length; distance between anterior margin and medial carina less than between posterior margin and medial carina; posterior margin with sparse setae on distal half. *Penes*: present. *Pleopod 2 appendix masculina*: extending beyond tip of endopod, 1.17× length of endopod; margins sinuate; slender; apex not at angle to adjacent margins, bluntly rounded. *Uropods*: exopod subequal to endopod, 0.91× the length of the endopod.

Additional descriptive characters. Based on holotype. *Body*: length c. 2.6× width. Colour translucent white to yellow in alcohol. Chromatophores present; large; grey-black in alcohol; arranged in bands. *Eyes*: with 7 ommatidia in horizontal diameter; with 7 ommatidia in vertical diameter; round; colour tan in alcohol. *Frontal lamina*: length c. 3.75× basal width; apex expanded, anterior margin angled. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 large pappose seta; article 3 short, subequal to article 1. Flagellum 10-articulate. *Antenna*: peduncular article 4 with 5 SS on posterolateral margin and 1 SS at anterodistal angle; article 5 with 2 pappose setae and 3 SS at posterodistal angle, c. 5 SS and 1 penicillate seta at anterodistal angle. Flagellum 21-articulate. *Mandible*: setal row with 16 RS. *Maxillule*: medial lobe with 3 large robust pappose setae and 2 small SS; lateral lobe with 12 RS on distal surface. *Maxilla*: lateral lobe with 4 SS; medial lobe with 5 SS and 10 PS; middle lobe with 12 long and 3 short SS. *Maxilliped*: endite with 1 coupling hook, and 5 PS. *Pereon*: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1; pereonites 1, 4–6 subequal and longest, 2–3 and 7 subequal. *Coxae*: pereonite 1, coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral

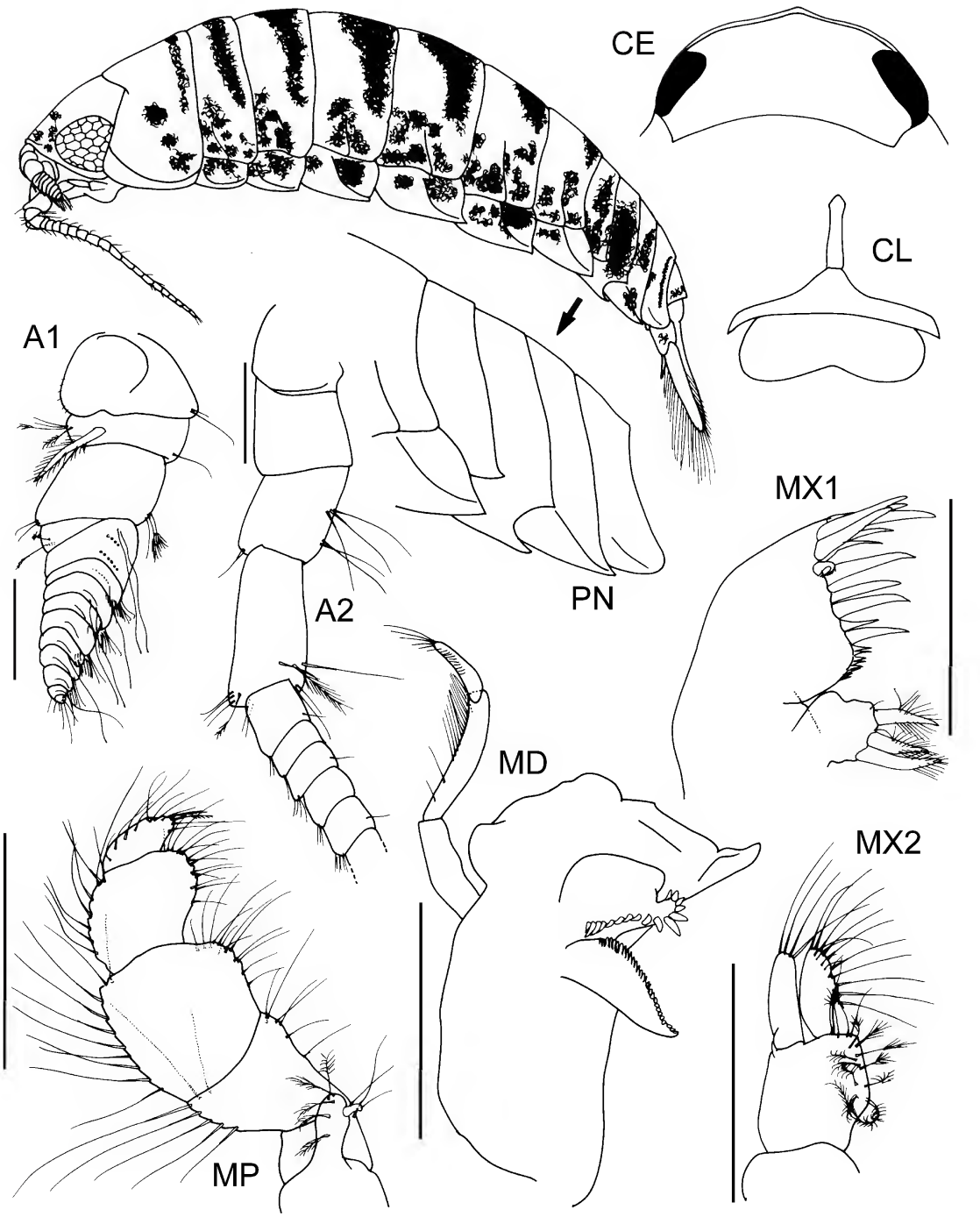

Fig. 51. *Natatolana zebra* n.sp., holotype. Scales = 0.5 mm.

corners. *Pleonite 2*: dorsal posterolateral margin subequal with ventral posterolateral margin. *Pereopod 7*: basis anterior margin straight; medial carina with PS along entire length; posterior margin convex, SS present. Ischium anterior margin with SS; posterior margin with groups of RS present, PS present. Merus anterior margin with 1 SS; posterior margin with 2 RS, SS present. Carpus posterior margin with 2 RS, SS absent. Propodus subequal to carpus; posterior margin with 2 RS, SS absent. *Penes*: forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally. *Pleopods 1–5*: exopod suture strongly developed on pleopods 1–5; endopod PS on most of margins on pleopods 1–4, absent on pleopod 5. *Uropods*: endopod triangular; medial margin convex, with 3 RS, PS along entire length; apex with 2 RS; lateral margin slightly convex, with 2 RS and 1 penicillate seta, PS along entire length. Exopod medial margin convex, with 3 RS, PS along entire length; apex acute, with 2 RS; lateral margin convex, with 6 RS, PS along entire length.

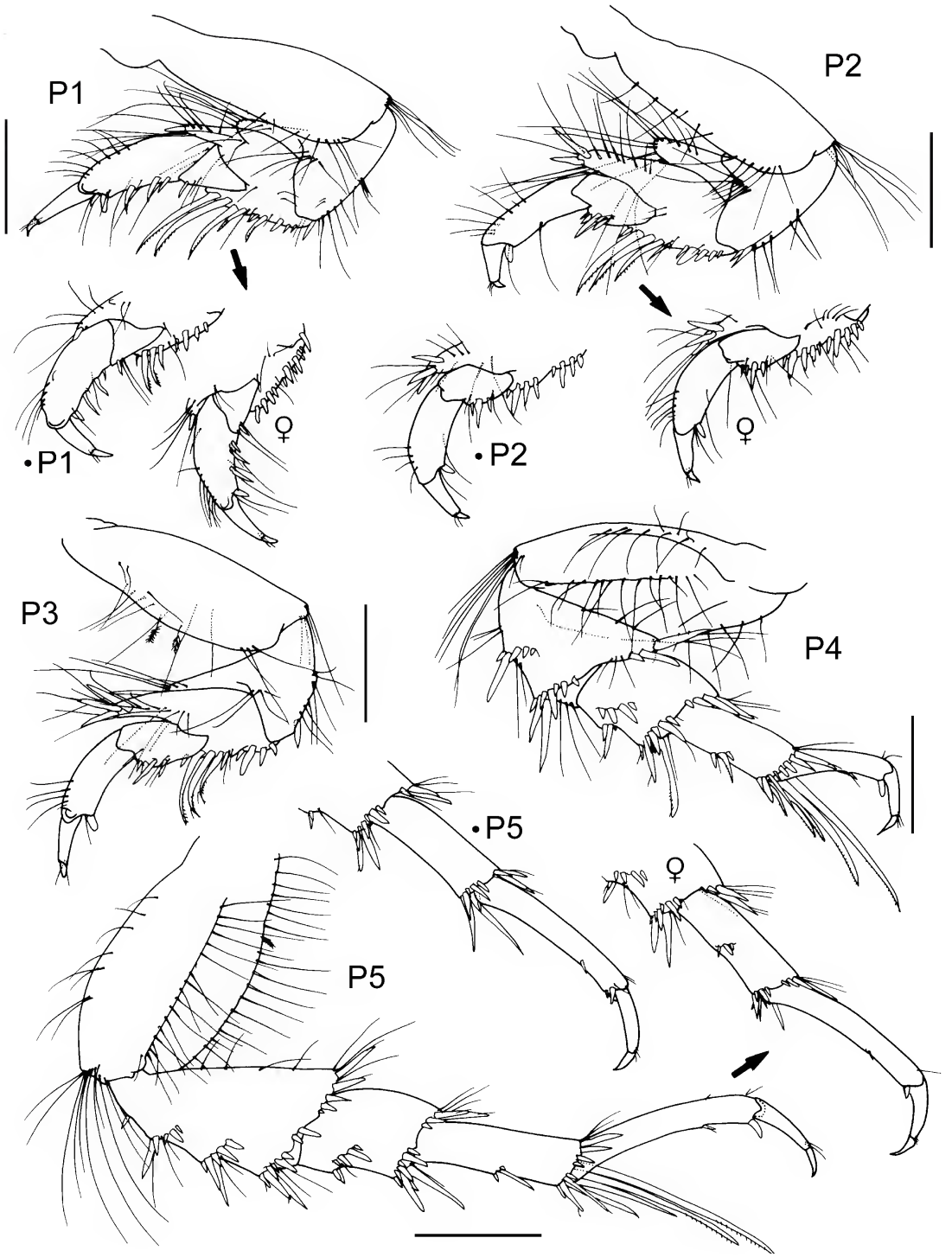

Fig. 52. *Natatolana zebra* n.sp., holotype, male, 11 mm except; •P5. = paratype male (immature) AM P47228; female = paratype female AM P47277. Scales = 0.5 mm.

Variation. Immature males lack the conspicuously elongate robust setae on pereopods 1–6.

Sexual dimorphism. Females lack the conspicuously elongated robust setae present on the merus of pereopods 1–3 and on the carpus of pereopods 4–6 of adult males.

Size. Up to c. 13.5 mm.

Etymology. Named after the equine quadruped, the zebra, in reference to the striped pattern of chromatophores.

Remarks. The most distinctive character that separates *Natatolana zebra* from other species of *Natatolana* is the elongate propodus of pereopod 5 (longer than that of pereopod 6 and twice as long as that of pereopod 7). The distinct dorsal depression on the pleotelson, presence of penes, lack of robust setae on the propodal palm of pereopod 2, relatively narrow basis of pereopod 7 and conspicuously long robust setae on pereopods 1–6 of males also help to distinguish this species from all others in the genus.

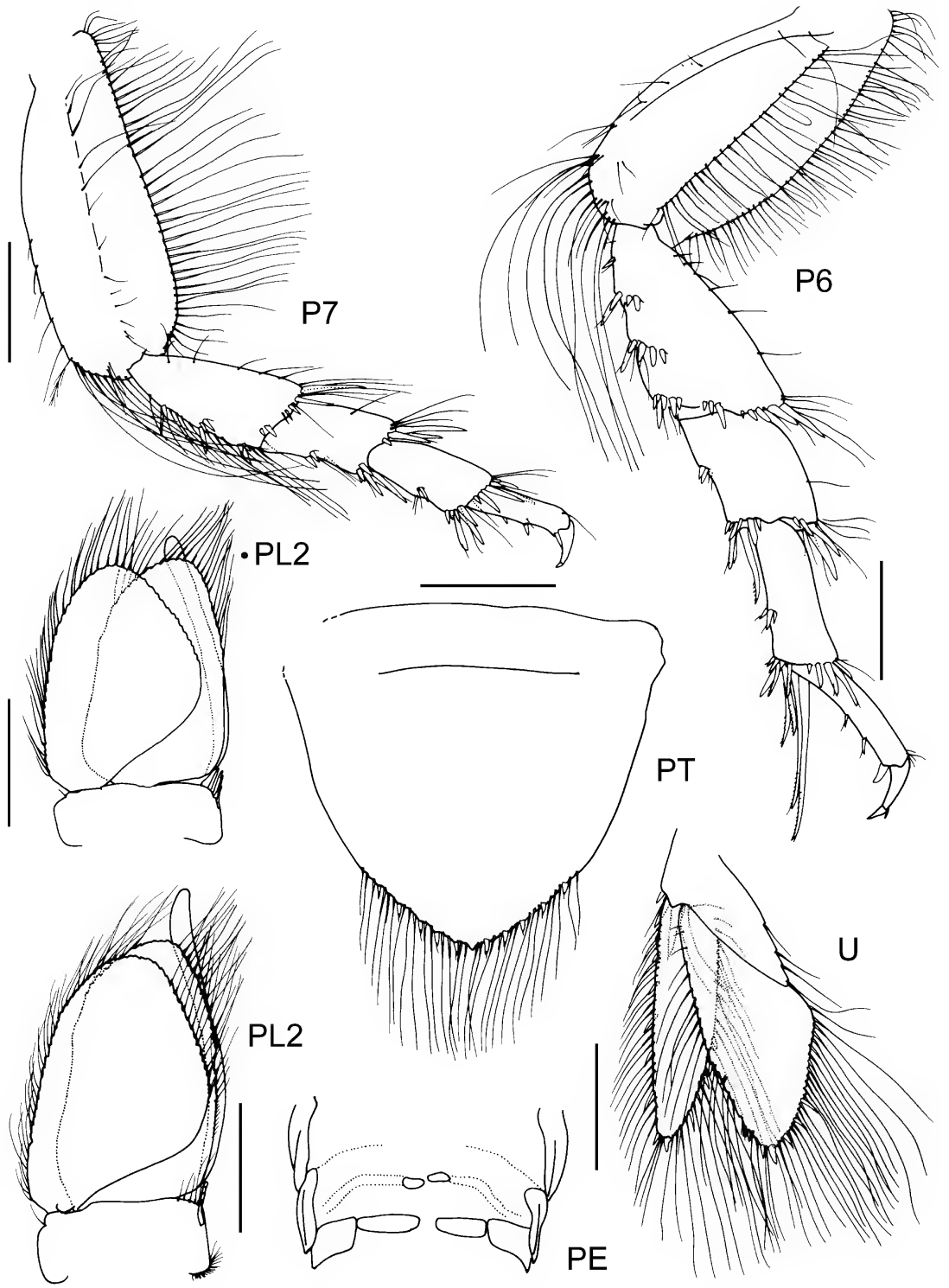

Fig. 53. *Natatolana zebra* n.sp., holotype, except; •PL2 = paratype male (immature) AM P47228. Scales = 0.5 mm.

Distribution and ecology. Australia: known only from southwest Tasmania in the vicinity of the type locality. At depths of 3–25 m. Scavenger.

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Laticauda frontalis (de Vis, 1905) and *Laticauda saintgironsi* n.sp. from Vanuatu and New Caledonia (Serpentes: Elapidae: Laticaudinae)—a New Lineage of Sea Kraits?

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ABSTRACT. The sea krait *Laticauda colubrina* is the most widespread member of its genus, extending from the Bay of Bengal through much of Asia and the Indo-Malayan Archipelago to New Guinea and many islands of the western Pacific Ocean. Unconfirmed records of the species may extend the range to the western coast of Central America. The species is subject to marked geographic variation in a number of morphological and meristic characters that have to date defied finer taxonomic resolution.

Two members of this complex previously subsumed under the specific name *colubrina* are here formally elevated to full species status. One species—*Laticauda saintgironsi* n.sp.—consists of those populations of *L. colubrina s.l.* found around the coast and in the coastal waters of the main island of New Caledonia. The second species—*Laticauda frontalis* (de Vis, 1905)—is a dwarf species found in sympatry and syntopy with *Laticauda colubrina* in Vanuatu and the Loyalty Islands of New Caledonia.

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Sea kraits are typically distinctively banded marine snakes that occur from the tropical western Pacific Ocean through the Papuan and Indo-Malaysian regions to the Philippines, the Ryukyu Archipelago and tropical southeast Asia to the Bay of Bengal (Smith, 1926), while McCarthy (1986) cites the following sources for records of one species (*Laticauda colubrina*) from the Pacific coasts of several Central American countries: Nicaragua (Villa, 1962), Mexico (Alvarez de Toro, 1982) and El Salvador (in a pers. comm. from J. Villa).

The phylogenetic and taxonomic status of this group of snakes has varied widely in the literature, but in the most recent phylogeny Scanlon & Lee (2004) place all proteroglyphous snakes within the family Elapidae and suggest that the *Laticauda* group is either a basal clade *within* an elapid subfamily (the Hydrophiinae) or a sister clade to the Hydrophiinae (and by inference a separate subfamily, the Laticaudinae). Earlier studies (e.g., McDowell, 1985, 1987; Cadle & Gorman, 1981; Greer,

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1998) present evidence for variations in this phylogenetic interpretation, and so we have somewhat arbitrarily treated this clade as a distinct subfamily, the Laticaudinae.

Until the present time, this family-level taxon was regarded as comprising three widely distributed species—*Laticauda colubrina* (Schneider, 1799), *L. laticaudata* (Linnaeus, 1758) and *L. semifasciata* (Reinwardt, 1837)—and two geographically restricted South Pacific species (the dwarf *Laticauda schistorhyncha* (Günther, 1874) endemic to Niue Island and the dwarf *Laticauda crockeri* Slevin, 1934 confined to Lake Tenggano on Rennell Island in the Solomon Islands). A further species (*Laticauda guineai*) was recently described from southern New Guinea (Heatwole *et al.*, 2005).

Since its establishment *L. schistorhyncha* has been treated as either a distinct species or as an isolated outlying Pacific subspecies of the predominantly Asian *Laticauda semifasciata*. As has been pointed out by McCarthy (1986) these two taxa are virtually identical in all morphological features other than size, so that some workers have regarded them as conspecific. However subsequent studies (in prep.) have shown that *L. schistorhyncha* is a distinctive dwarf species that appears to breed only on the small, isolated mid-oceanic island of Niue. We here regard it as a distinct species constituting, with *L. semifasciata*, a separate and distinctive lineage within the genus *Laticauda*, to which Kharin (1984) has assigned the subgeneric name *Pseudolaticauda*.

Historic records (Smith, 1926; McCarthy, 1986) and cited widespread distributions of this (Golay *et al.*, 1993) and other laticaudine species from elsewhere in the Pacific, including high latitude sites in New Zealand (McCann, 1966), Tasmania (Lord, 1919) and the coast of mainland eastern Australia (Smith, 1926; McCarthy, 1986; Cogger, 1975) almost certainly represent waif individuals carried by storms and/or currents away from their normal (i.e. preferred) ranges. In most cases individuals are permanently removed, geographically and reproductively, from other members of their species and so are lost to the gene pool. Extensive surveys of the Pacific Islands over the past 40 years have failed to reveal any reproducing populations of *Laticauda schistorhyncha* beyond the coastal waters of Niue. Only a handful of records of other laticaudine species are known from eastern Australia over the past two centuries, and no resident populations are known from Australian tropical or temperate continental waters, despite the presence of substantial communities of *Laticauda guineai* in nearby coastal areas of the continuous continental shelf shared with southern Papua New Guinea.

While the data are fragmentary, all Pacific studies of *Laticauda colubrina s.l.* to date, based on morphological variation (McCarthy, 1986; Heatwole *et al.*, 2005), mark/recapture data (Guinea, 1986; Shetty, 2000), toxin chemistry and structure (Tamiya, 1985) and genetic analysis (Slowinski & Keogh, 2000) indicate that laticaudines, both individuals and local populations, display extremely high site fidelity to particular island reef systems, with little gene flow across open seas even when such systems are geographically proximate.

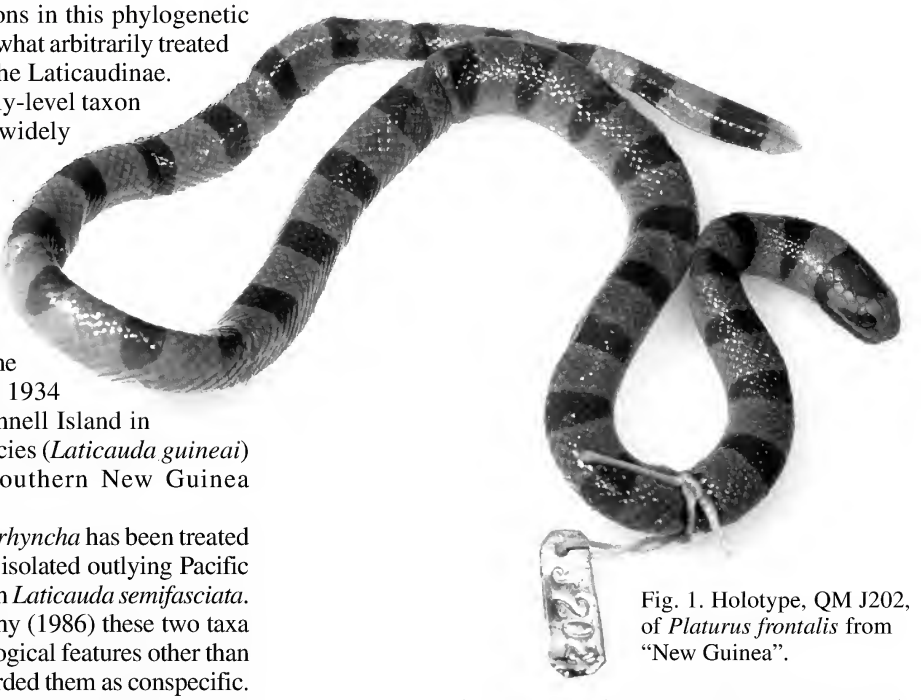

Fig. 1. Holotype, QM J202, of *Platurus frontalis* from "New Guinea".

The yellow-lipped sea krait, *Laticauda colubrina s.l.* is one of the world's most widely distributed snakes. Resident, reproducing populations range from the Bay of Bengal through the warmer parts of east and southeast Asia to the islands of the western Pacific Ocean (Smith, 1926). It is subject to considerable geographic variation in external morphological features (McCarthy, 1986), with clear mean regional differences in some external characters.

Enderman (1970) recognized six distinctive populations which he regarded as warranting subspecific recognition, including one from New Caledonia (here described as a new species, *saintgironsi*, below), one from Vanuatu (here shown to represent two distinct species, *frontalis* and *colubrina*), and one from Fiji (here also assigned to *colubrina*). Published studies of venom chemistry (Tamiya *et al.*, 1983), karyology (Gorman, 1981), and molecular data (Cadle & Gorman, 1981; Keogh *et al.*, 1998; Slowinski & Keogh, 2000) did not identify any significant species-level variation within the *colubrina* complex.

A cladistic analysis by McCarthy (1986), that included the five species of *Laticauda* then recognized as valid, produced conflicting associations of the monotypic *L. colubrina* clade with either the *L. laticaudata* clade (with two included species) or with the *L. semifasciata* clade (also with two included species). However in his phenetic analysis of 65 character states, *colubrina* is clearly associated with the *laticaudata* lineage. McCarthy concluded that while there are three distinct lineages, *L. colubrina* "... appears to be, in some ways, transitional between the *L. laticaudata* lineage and the divergent *L. semifasciata* lineage ... ".

The purpose of this paper is to formally redefine and diagnose *Laticauda frontalis*, to describe and name what we regard as its probable sister species (*Laticauda saintgironsi*), and so provide a diagnosis of a probably new clade within this previously monotypic lineage. A key to the species in the *Laticauda colubrina* complex, incorporating the two species that are the subject of this paper, is provided in Heatwole *et al.* (2005).

Materials and methods

Most of the specimens listed in this paper were collected by the authors in the field and most linear measurements, weights and scale counts were made at that time on either living (including specimens released back into the wild), anaesthetized or freshly euthanased snakes. Linear measurements were made using either a steel tape or vernier calipers. Weights were taken using Pesola spring balances of a range appropriate to the size of an individual snake. Heart position was clearly visible as a strong pulse that lifted the adjacent ventral scales when a snake was laid on its back.

Statistical analyses were undertaken using the SYSTAT 10 statistical package. Differences in regression slopes between species were determined by general linear models, including the terms species, body length and the species times body length interaction. A significant interaction term was indicative of a significant difference in the regression slopes between the different species/populations. The upper limits of the graphs in Figs. 4–7 were determined by the largest specimen examined, the same scale being used on each graph to facilitate visual comparisons of the curves of individual species/populations and sexes. However the regressions of the compared curves were calculated for only that part of each graph covering the available range of values.

Further, because geographic variation in such a wide-ranging taxon as *Laticauda colubrina s.l.* is considerable (McCarthy, 1986; Heatwole *et al.*, 2005), we have limited our definitions of both species, including the paratypic series for *L. saintgironsi* below, almost entirely to specimens that we have ourselves collected and that we can assign confidently to the relevant taxon. We have identified other specimens in museum collections around the world as belonging to these species (some only tentatively, see Heatwole *et al.*, 2005), but we have deliberately avoided assigning type status to these other specimens.

Laticauda frontalis (de Vis, 1905)

From the time of its original description by Charles de Vis (1905) from a single juvenile, subsequent authors assigned his *Platurus frontalis* to the synonymy of *Laticauda colubrina*. The first published indication that this species represented a valid species is a statement by McCarthy (1986) that he had been advised by one of the present authors (HGC) that we had recognized from Vanuatu a "new form", smaller than and distinct from *L. colubrina*, to which McCarthy assigned one of his specimens. The name *Laticauda frontalis* was first used as the name of a valid species (but not diagnosed) by Cogger *et al.* (1987) in a paper devoted to a member of the *laticaudata* clade (*Laticauda crockeri*), while Greer (1998), in the absence of any published diagnosis, indicated that *frontalis* was valid but yet to be defined.

This species has long been confused with *L. colubrina s.l.* because they are both morphologically similar, geographically sympatric and ecologically syntopic. The two species occupy the same terrestrial and marine habitats, share the same prey, and even aggregate in the same shelter sites. As defined below, *Laticauda frontalis* is a highly distinctive dwarf species apparently confined to Vanuatu and the Loyalty Islands, despite its type locality of "New Guinea".

However, because *L. frontalis* occurs in much lower numbers than *L. colubrina* throughout the former's known range (a *frontalis:colubrina* ratio of 96:184 is found in our 280 Vanuatu field records), the lack of sampling at the northern end of the known geographic range of *frontalis* means that the northern limit of that range is unknown.

More recently the present authors, having resolved the taxonomic problems arising from the sympatry and syntopy of this cryptic species with the larger, morphologically similar *colubrina*, pointed out to colleagues that exploiting identical or overlapping feeding and resting habitats and food sources presented a variety of ecological and evolutionary challenges. What are the mechanisms whereby these resources are shared or partitioned, and the reproductive integrity of each species maintained,. These aspects have been the subject of several recent studies (Shine *et al.*, 2002a,b; Reed *et al.*, 2002).

Following is a formal redescription of:

Laticauda frontalis (de Vis, 1905)

Platurus frontalis de Vis, 1905. A new genus of lizards. Annals of the Queensland Museum, 6:48. Holotype: Queensland Museum (QM) J202 (Fig. 1). Type locality: New Guinea. Date of collection, donor and/or collector unknown.

Diagnosis. A banded sea krait of the genus *Laticauda* characterized by the possession of a yellow upper lip, an undivided rostral scale, an almost invariate 21 mid-body scale rows in both sexes, fewer than 209 (males) and 212 (females) ventral scales, and a maximum snout-vent length (SVL) of 654 mm (males) and 783 mm (females). It can be distinguished from *L. laticaudata* and *L. crockeri* by its yellow upper lip (black in *laticaudata* and *crockeri*) and from *L. semifasciata* and *L. schistorhyncha* by its undivided rostral. From *L. colubrina* it may be distinguished by the following combination of characters: a lower modal mid-body scale row count of 21, lower ventral scale counts in both sexes (Table 1, Fig. 9), smaller size (Table 1) and, throughout the known area of sympatry, by the absence of a lower lateral connection between the black head band and the first black band on the neck (Fig. 2), and the failure of the dark body bands, at least anteriorly, to extend to the middle of the venter (Fig. 1).

Description of the holotype. A member of the *Laticauda colubrina* complex in shape; the mid-body diameter is contained 40.7 times in its snout-vent length and the head is scarcely wider than the neck. Head width (widest point) 7.3 mm, head length (snout tip to rear edge of quadrate) 8.9 mm, the latter representing 3.0% of snout-vent length. Rostral undivided, as broad as deep, and separating the nasals. Internasals narrowly in contact behind the rostral, while there is a large azygous scale, almost as large as a prefrontal, separating the prefrontals. Frontal 2.25 times longer than broad, while each supraocular is about the same width as the frontal. Seven supralabials on each side, the second and third contacting the eye. Nine infralabials on each side, the count being confused by a series of splint-like marginal scales separating the anterior infralabials from the lip margins. Temporals 1 + 3 on each side. Postmental scale (*sensu* McCarthy, 1986) absent.

Number of scale rows around the body (excluding the ventrals) at the 20th, 50th, 100th, 150th and 200th ventrals

Table 1. Interspecific and sexual variation in key external meristic and morphological characters for *Laticauda frontalis* and *Laticauda saintgironsi* (upper) and for Vanuatuan and Fijian populations of *Laticauda colubrina* (lower). * Number at 100th ventral.

character	*L. frontalis* males				*L. frontalis* females				*L. saintgironsi* males				*L. saintgironsi* females			
	n	range	mean	SD	n	range	mean	SD	*n*	range	mean	SD	*n*	range	mean	SD
snout-vent length (mm)	49	339–654	542.3	51.00	21	293–783	605.1	130.00	79	350–817	694.3	80.80	34	361–1090	782.9	165.13
tail length (mm)	49	46–171	78.8	17.60	21	34–122	66.7	17.20	78	48–125	78.9	13.20	34	42–110	84.2	15.49
mid-body scale rows (*No.**)	38	19–21	20.9	0.03	18	21–23	21.1	0.47	26	21–25	21.2	0.54	26	21–25	21.6	1.03
ventral scales (*No.*)	38	192–208	198.4	3.32	18	199–211	204.3	3.09	26	211–224	217.3	3.60	26	215–230	222.4	3.55
subcaudal scales (*No.*)	37	34–41	37.4	1.64	18	29–34	31.1	1.37	25	37–42	38.7	1.49	25	25–34	30.8	1.80
weight (g)	49	20–139	76.7	20.98	19	38–165	99.4	40.30	71	18–234	157.2	38.61	24	20–650	248.1	163.52
dark body bands (*No.*)	38	27–37	32.0	2.27	18	29–41	33.4	2.97	26	23–29	26.8	1.75	26	21–30	25.6	2.02
dark tail bands (*No.*)	37	3–4	3.9	0.46	18	3–4	3.1	0.236	26	3–4	3.3	0.49	26	2–3	2.4	0.50

character	*L. colubrina* males (Vanuatu)				*L. colubrina* females (Vanuatu)				*L. colubrina* males (Fiji)				*L. colubrina* females (Fiji)			
	n	range	mean	SD	*n*	range	mean	SD	*n*	range	mean	SD	*n*	range	mean	SD
snout-vent length (mm)	43	588–893	720.7	65.72	59	134–1450	774.5	316.32	53	333–928	688.8	169.79	36	340–1325	867.6	275.86
tail length (mm)	41	75–133	110.6	13.44	59	13–191	82.1	34.37	53	44–152	107.2	30.97	36	40–140	95.1	29.56
mid-body scale rows (*No.**)	34	23–24	23.1	0.29	29	23–27	24.0	0.85	52	23–25	23.0	0.28	36	23–25	23.8	0.93
ventral scales (*No.*)	76	216–234	223.9	3.49	64	202–239	229.6	5.27	52	215–232	221.9	3.70	36	217–232	227.5	3.71
subcaudal scales (*No.*)	71	37–46	42.4	1.64	62	26–39	33.5	1.90	50	37–45	41.8	1.74	36	29–36	32.5	1.70
weight (g)	55	18–308	143.7	50.23	63	18–1560	257.7	313.21	44	15.3–500	227.9	115.42	32	19.2–1110	404.4	305.88
dark body bands (*No.*)	54	29–36	32.8	1.75	55	29–36	33.0	1.64	52	23–33	27.5	1.98	36	24–33	26.9	2.01
dark tail bands (*No.*)	52	3–5	4.1	0.46	54	2.5–5	3.3	0.49	52	3–5	4.0	0.31	36	1–4	3.0	0.41

respectively are 21, 21, 21, 21, and 19. There are 203 ventral scales (gastrosteges) and 31 divided subcaudal scales, indicating that it is a female (specimen not dissected). The snout-vent length is c. 293 mm (several counts; the specimen is badly kinked in preservation) while the tail length is 34 mm.

Thirty-one dark body bands and 3 dark caudal bands; the first body band is not connected laterally to the nuchal band (see Fig. 2, upper). This is the smallest specimen of this species seen by the authors, and possesses the characteristic juvenile condition of ventrally incomplete dark cross-bands, the latter generally extending only to the middle or lower parts of the flanks.

Variation. Variation in a number of phenotypic character states in *Laticauda frontalis* is compared in Table 1 with variation in the same characters for syntopic *Laticauda colubrina* (from Vanuatu), for *Laticauda colubrina* from the Fiji Islands to the east, and from *Laticauda saintgironsi* from New Caledonia to the south.

The extent to which the dark bands fail to meet ventrally varies ontogenetically. All dark bands are usually incomplete in juveniles and subadults, while in large adults usually only those bands on the anterior part of the body may remain incomplete.

The centre of the heart is located between ventrals 67 and 75 (mean = 70.6, SD = 2.37, n = 10).

Distribution. The holotype of *Laticauda frontalis* is said to have come from "New Guinea"; if this provenance is correct then it is the only specimen currently known outside the region encompassing Vanuatu and the Loyalty Islands. P. Couper (*in litt.*) of the Queensland Museum advises that there is no additional documentation associated with the holotype's original acquisition that might provide more accurate information about its provenance (including any doubt or uncertainty) or the unknown donor/collector. All of our field-acquired specimens were collected on two island complexes—Efate and Espiritu Santo—in the Republic of Vanuatu (formerly the British-French condominion of the New Hebrides).

There is a single specimen in the Macleay Museum, University of Sydney (MM 633) and another in the Muséum national d'Histoire naturelle, Paris (HFH) from the Loyalty Islands (the easternmost islands of New Caledonia located about one-third of the distance between New Caledonia's main island (*Grande Terre*) and the southernmost islands of Vanuatu). The species has not been recorded from the Solomon Islands to the northwest of Vanuatu, nor from New Caledonia's main island complex. Consequently we regard the current distribution of the species to be confined to the Loyalty Islands and the islands of Vanuatu, at least as far north as the island of Espiritu Santo. And in the absence of any records of this species from New Guinea since it was described in 1905, and without secondary sources to confirm the original type locality, we regard either the type locality of "New Guinea" to be erroneous or the holotype to be a waif individual originating from the Vanuatu region. In all of the features used above to characterize this species, the holotype falls within the range of variation recorded in specimens from Vanuatu.

Ecology. Like other members of the *Laticauda colubrina* species complex, *Laticauda frontalis* feeds exclusively on eels belonging to several families—most commonly those in the families Muraenidae and Congridae (Reed *et al.*, 2002).

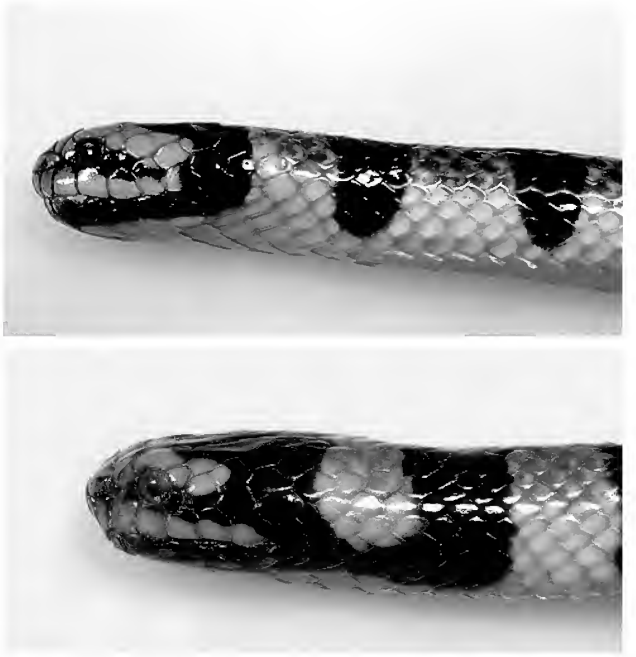

Fig. 2. Lateral head pattern diagnostic of sympatric populations of *Laticauda frontalis* (upper) and *Laticauda colubrina* (lower) in Vanuatu. Note that the nuchal band is never linked, laterally, to the first body band in *L. frontalis* and very rarely unlinked in Vanuatuan *L. colubrina*.

This species was long confused with juveniles and subadults of the sympatric and syntopic *Laticauda colubrina*, not only because of their morphological similarity but in large part because the two species could be found together, both in terrestrial aggregations and in aquatic feeding sites. On some small coral islets within the lagoon at Panangisu on the northern side of Efate Island in Vanuatu, individuals of both species were found coiled up together under the same rock or pile of decaying vegetation, or in wave-eroded cavities and crevices in the exposed perimeter calcarenitic rock above high tide level but well within the splash zone.

Other individuals were found in cavities in the wide, flat calcarinite platforms that make up the supralittoral zone around many parts of the larger islands, even close to major urban centres such as the national capital of Port Vila, on Efate Island. At night the snakes could be found emerging from the sea onto these platforms, or moving across them 100 m or more from the sea.

Maximum prey size is broadly correlated with body size in anguillophagous sea kraits, and so the dwarf *frontalis* competes for prey with similar-sized (generally sub-adult) members of the larger syntopic *Laticauda colubrina* (Shine *et al.*, 2002b).

Material examined. Numerous live specimens captured for venom extraction were examined for a variety of mensurable and meristic characters before being released back into the wild. Heatwole *et al.* (2005) list additional specimens examined by only one of us (HFH) in other museum collections, but the following specimens assigned by us to this species were preserved and lodged in the herpetological collections of the Australian Museum, Sydney: R164858–68♂♂, R164869–70♀♀, R164871♂, R144025♀, R144026–28♂♂, R144055♂ from Pango Point at Pango (Etang) Village, near Port Vila, Efate Island, Vanuatu; R164872–79♂♂, R144020♀, R144021–22♂♂ from Niogoriki Island, off Paunangisu Village, N. coast of Efate Island, Vanuatu; R164880–81♂♂, from W. side of Mele Bay, Port Vila, Efate Island, Vanuatu; 144023♀, 144024♂, from Tukutuku Plantation, Tukutuku Bay, Efate Island, Vanuatu.

Laticauda saintgironsi n.sp.

Holotype. Australian Museum, Sydney (AMS) R162999 (AMS field no. 34602), an adult male from Porc-épic Island, Le Lagon, near Noumea, New Caledonia collected by the authors on 14 September 1993, 22°19'45.6"S 166°34'08.5"E.

Paratypes. All paratypes are from localities within New Caledonia and are lodged in the Australian Museum, Sydney (AMS): R78031♂, R78032♀, R78035–38♀♀, R78042♀, R78043♂, R78046♀ from Île Mouac; R109668♂, R109669–70♀♀, R109671–73♂♂, R109674♀, R109690♂, R109691♀, R109692♂, R109693♀, R109694–98♂♂, R109699♀ from Île Redika; R109681♀, R109682–83♂♂, R109684♀, R109685♂, R109686♀, R109687♂, R109688 i, R109689♀ from Île Grand Mato; R109623–24♀♀, R109625♂, R109659♂, R109660–62♀♀, R109663♂, R109664♀, R109665♂, R109666♀; R164882–83♂♂, R164884♀, R164885–86♂♂, R164887♀, R164888 i, R164889–93♂♂, R164894♀, from Île Porc épic, near Noumea; R78086♂ from Île Noue; R144070–71♀♀, R144072–73♂♂ from near Ouenguie Village, c. 20 km north of Hienghene; R144065♂ from south of Mou, east coast; R144069♂ from c. 5 km SE of Koulnoue Village, near Hienghene; R144094–96♂♂ from near Malabou Beach Hotel, Baie de la Nehoue, c. 5 km S of Poum. The letter i refers to immature/indeterminate specimens.

Other specimens examined included living individuals that were weighed, measured and scalation examined before being released back into the wild; other specimens examined by one of the authors (HFH) are listed and discussed in Heatwole *et al.* (2005).

Diagnosis. A banded sea krait of the genus *Laticauda* characterized by the possession of a yellow or cream upper lip, an undivided rostral scale, usually 21 mid-body scale rows in both sexes (but occasionally 23 or rarely 25 rows, mode 21 in both sexes), ventral scales from 211 to 224 in males and from 215 to 230 in females, and a maximum snout-vent length (SVL) of 817 mm (males) and 1090 mm (females). It can be distinguished from *L. laticaudata* and *L. crockeri* by its yellow upper lip (black or dark brown in *laticaudata* and *crockeri*) and from *L. semifasciata* and *L. schistorhyncha* by its pale upper lip and undivided rostral (upper lip brown and rostral divided in *semifasciata* and *schistorhyncha*).

From the nearest populations (Fiji and Vanuatu) of its allopatric congener *L. colubrina* it may be distinguished by a lower modal mid-body scale row count of 21, its lower ventral scale counts (Table 1, Fig. 8); smaller size (Table 1); dark body bands either not meeting ventrally or narrowing ventrally, often with a pale mid-ventral blotch; and its distinctive body colour in which the paler bands are predominently brown (fawn to rich russet *vs* steely grey or blue in *L. colubrina*).

From *L. frontalis* is may be distinguished by its larger size and higher ventral and subcaudal counts (Table 1) and the distinctive brown dorsal colour (grey or blue-grey in *frontalis*).

Description of the holotype. A typical member of the *Laticauda colubrina* complex in shape, with a relatively slender body in which the mid-body diameter is contained 33.3 times in its snout-vent length and the head is scarcely

wider than the neck. Head width (widest point) 16.2 mm, head length (snout tip to rear edge of quadrate) 21.8 mm, the latter representing 3.0% of snout-vent length. The rostral is undivided, about as broad as deep, and separates the nasals, each of which contacts the single preocular scale on each side. The internasals are about as large as the prefrontals, meeting broadly in the middle. The prefrontals are separated posteriorly by a large azygous scale, about equal in size to one of the internasals. A single, large supraocular scale on either side of the frontal. The latter is only slightly longer than broad. Six supralabials on each side, the third and fourth entering the eye. One anterior temporal scale on each side, and two posterior temporals. Six or seven infralabials, though the counts are uncertain because all but the first three infralabials are excluded from the lip by an irregular series of splint-like marginal scales.

There are 21 mid-body scale rows. Body scale row numbers are reduced only posteriorly, with 21 rows at the 20th, 50th, 100th and 150th ventrals and 19 rows at the 200th ventral. There are 218 ventral scales and 38 pairs of subcaudal scales. The snout-vent length (SVL) in life was 727 mm, while the tail length was 88 mm. The live weight was 185 g.

The colour pattern (Figs. 2 and 3) consists of a broad black band across the back of the head, extending forward to about the middle of the frontal scale; this band is joined laterally on each side by a broad dark stripe from behind the eye and another continuous black stripe below each lower jaw. At the point where these all meet there is a broad lateral black bar linking the dark head band to the first neck band. There are 28 black bands on the trunk and four on the tail. All of these black bands extend right around the body, but most trunk bands also have a pale, mid-ventral blotch. Along the vertebral line the pale bands between the black bands are 60–66% as wide as the black bands.

In life, the colour of the holotype from above was bright russet-orange, fading gradually on the flanks to a pale cream or white, but with many of the individual scales tipped or edged with black or dark blue-grey, giving the pale bands a reticulated appearance; the dark bands were glossy black. Ventrally the colour was creamy-white, with the margins of the ventral scales slightly darker-edged with pale brown. Most of the scales on the head and lips are finely margined with black, emphasizing the sutures.

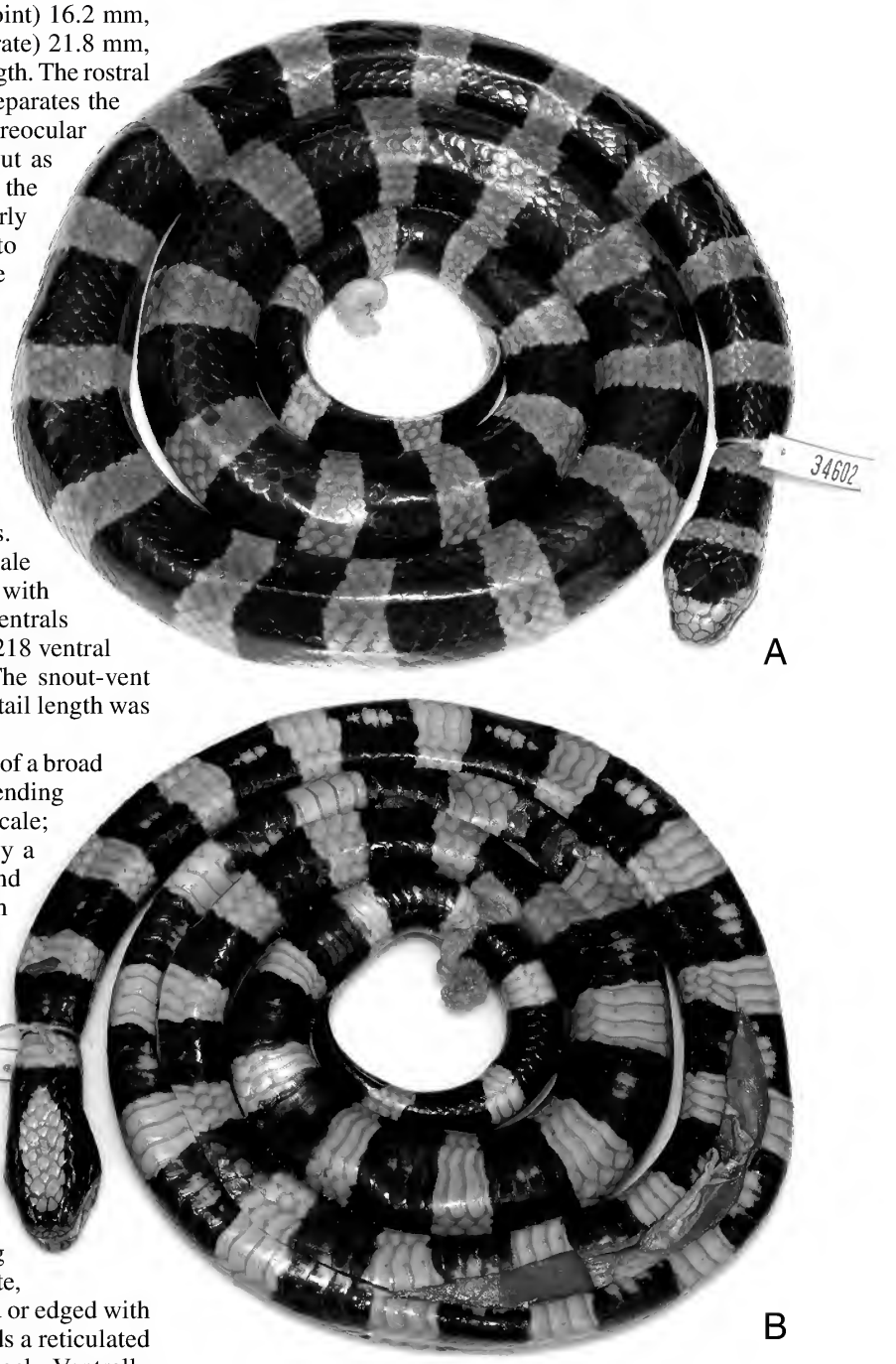

Fig. 3. (*A*) Dorsal view of holotype, AM R162999, *of Laticauda saintgironsi* from Porc-épic Island, Le Lagon, near Noumea, New Caledonia. (*B*) Ventral view of holotype, AM R162999, *of Laticauda saintgironsi* from Porc-épic Island, Le Lagon, near Noumea, New Caledonia.

Variation. The general appearance and non-diagnostic scalation varies little from that described for the holotype above. As in all *Laticauda* there is marked sexual dimorphism in body mass and relative tail length, sometimes exaggerated in older (larger) individuals Variation in those principal morphological characters used in diagnosing the species are given in Table 1 and Figs. 4–7. In both cases the variables for *Laticauda saintgironsi* are compared with those in adjacent regional populations of both *Laticauda colubrina* and *Laticauda frontalis*.

The number of scale rows around the body (excluding the ventrals) varies along the length of the body, as shown in Table 1 for (usually) five points along the body—at the 20th, 50th, 100th, 150th and either the last or 200th ventral (whichever came first), but the mid-body count is mostly 21 in males and females (Fig. 9) and only occasionally 23 or 25. The ventral scales range from 211–230 (Table 1, Fig. 8) and the paired subcaudal scales range from 25–42 (37–

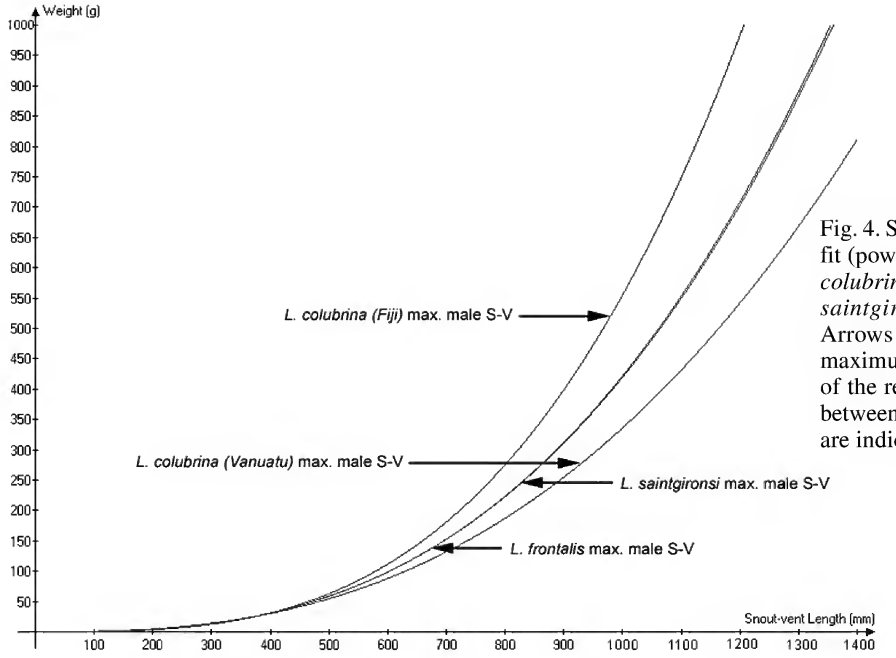

Fig. 4. Snout-vent length *vs.* live body weight best fit (power) regression curves for male *Laticauda colubrina* (Fiji and Vanuatu), *L. frontalis* and *L. saintgironsi* from the western Pacific region. Arrows indicate points on curves representing maximum snout-vent lengths attained by males of the respective species. Significant differences between the slopes of the following pairs of curves are indicated in bold type:

L. saintgironsi vs. *L. frontalis*	$F_{1-112} = 3.704$	$p = 0.057$
***L. saintgironsi* vs. *L. colubrina* (Fiji)**	**$F_{1-111} = 19.932$**	**$p < 0.001$**
L. saintgironsi vs. *L. colubrina* (Vanuatu)	$F_{1-109} = 2.128$	$p = 0.147$
L. colubrina* (Fiji) vs. *L. frontalis	**$F_{1-85} = 4$**	**$p < 0.001$**
***L. frontalis* vs. *L. colubrina* (Vanuatu)**	**$F_{1-83} = 5.561$**	**$p = 0.021$**
L. colubrina (Fiji) vs. *L. colubrina* (Vanuatu)	$F_{1-82} = 2.727$	$p = 0.103$

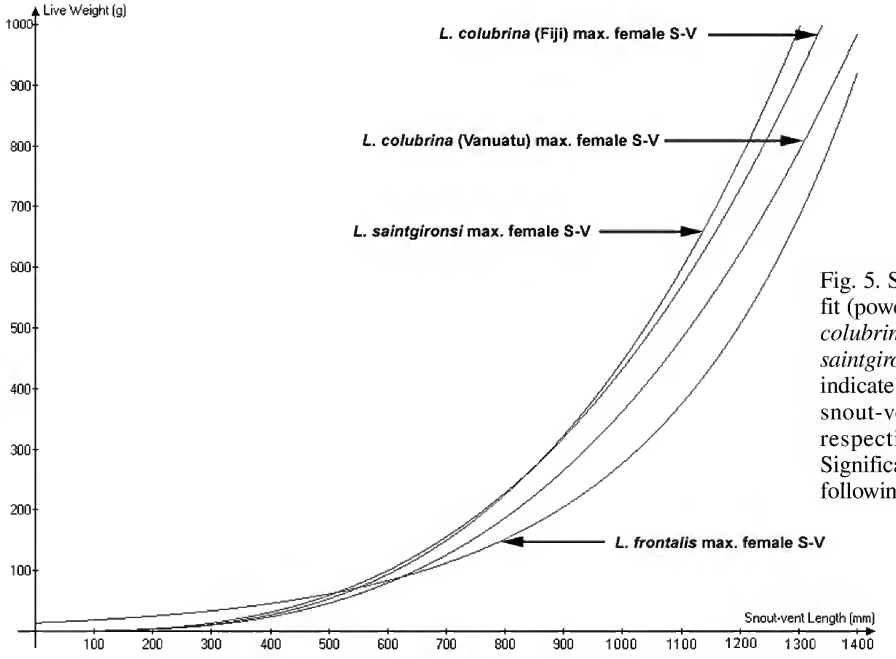

Fig. 5. Snout-vent length *vs.* live body weight best fit (power) regression curves for female *Laticauda colubrina* (Fiji and Vanuatu), *L. frontalis* and *L. saintgironsi* from the western Pacific region. Arrows indicate points on curves representing maximum snout-vent lengths attained by females of the respective species. Axes scales as in Fig. 4. Significant differences between the slopes of the following pairs of curves are indicated in bold type:

L. frontalis* vs. *L. saintgironsi	**$F_{1-40} = 13.783$**	**$p = 0.001$**
L. saintgironsi vs. *L. colubrina* (Fiji)	$F_{1-55} = 3.582$	$p = 0.064$
L. saintgironsi vs. *L. colubrina* (Vanuatu)	$F_{1-78} = 1.791$	$p = 0.185$
***L. frontalis* vs. *L. colubrina* (Fiji)**	**$F_{1-49} = 9.129$**	**$p = 0.004$**
***L. frontalis* vs. *L. colubrina* (Vanuatu)**	**$F_{1-72} = 7.102$**	**$p = 0.009$**
L. colubrina (Fiji) vs. *L. colubrina* (Vanuatu)	$F_{1-87} = 0.767$	$p = 0.384$

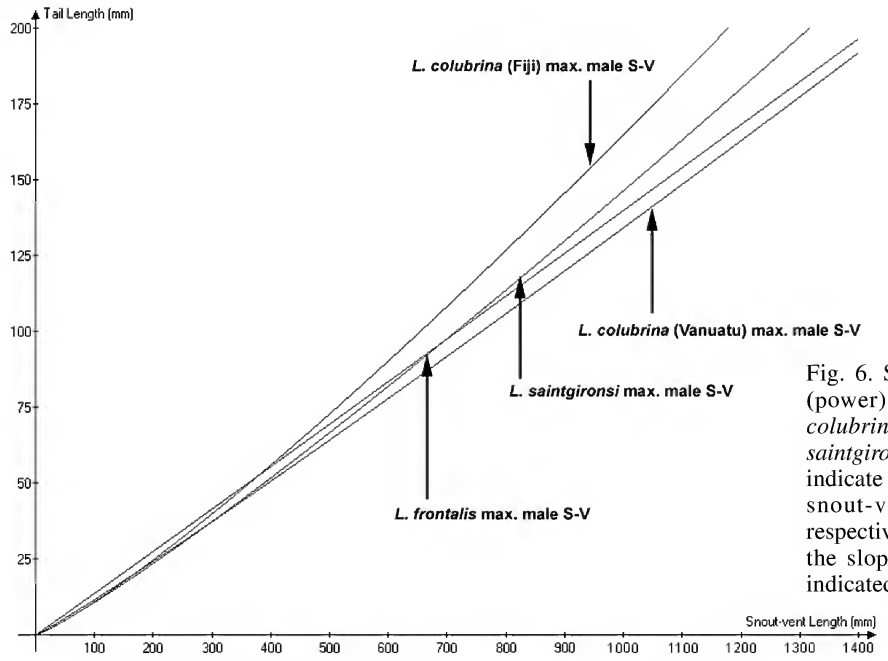

Fig. 6. Snout-vent length *vs.* tail length best fit (power) regression curves for male *Laticauda colubrina* (Fiji and Vanuatu), *L. frontalis* and *L. saintgironsi* from the western Pacific region. Arrows indicate points on curves representing maximum snout-vent lengths attained by males of the respective species. Significant differences between the slopes of the following pairs of curves are indicated in bold type:

L. saintgironsi vs. *L. frontalis*	$F_{1-52} = 0.213$	$p = 0.647$
***L. colubrina* (Fiji) vs. *L. colubrina* (Vanuatu)**	**$F_{1-85} = 133.073$**	**$p < 0.001$**
L. saintgironsi vs. *L. colubrina* (Vanuatu)	$F_{1-92} = 2.578$	$p = 0.112$
L. colubrina* (Fiji) vs. *L. frontalis	**$F_{1-69} = 49.749$**	**$p < 0.001$**
L. frontalis vs. *L. colubrina* (Vanuatu)	$F_{1-76} = 0.336$	$p = 0.564$
***L. colubrina* (Fiji) vs. *L. colubrina* (Vanuatu)**	**$F_{1-109} = 56.594$**	**$p < 0.001$**

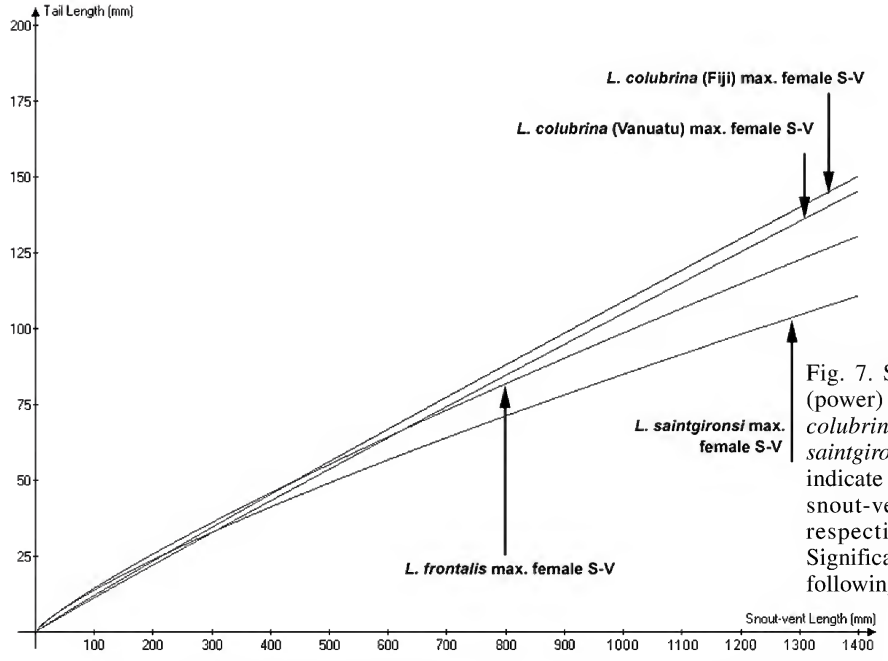

Fig. 7. Snout-vent length *vs.* tail length best fit (power) regression curves for female *Laticauda colubrina* (Fiji and Vanuatu), *L. frontalis* and *L. saintgironsi* from the western Pacific region. Arrows indicate points on curves representing maximum snout-vent lengths attained by females of the respective species. Axes scales as in Fig. 6. Significant differences between the slopes of the following pairs of curves are indicated in bold type:

L. saintgironsi vs. *L. frontalis*	$F_{1-52} = 0.213$	$p = 0.647$
***L. colubrina* (Fiji) vs. *L. colubrina* (Vanuatu)**	**$F_{1-85} = 133.073$**	**$p < 0.001$**
L. saintgironsi vs. *L. colubrina* (Vanuatu)	$F_{1-92} = 2.578$	$p = 0.112$
L. colubrina* (Fiji) vs. *L. frontalis	**$F_{1-69} = 49.749$**	**$p < 0.001$**
L. frontalis vs. *L. colubrina* (Vanuatu)	$F_{1-76} = 0.336$	$p = 0.564$
***L. colubrina* (Fiji) vs. *L. colubrina* (Vanuatu)**	**$F_{1-109} = 56.594$**	**$p < 0.001$**

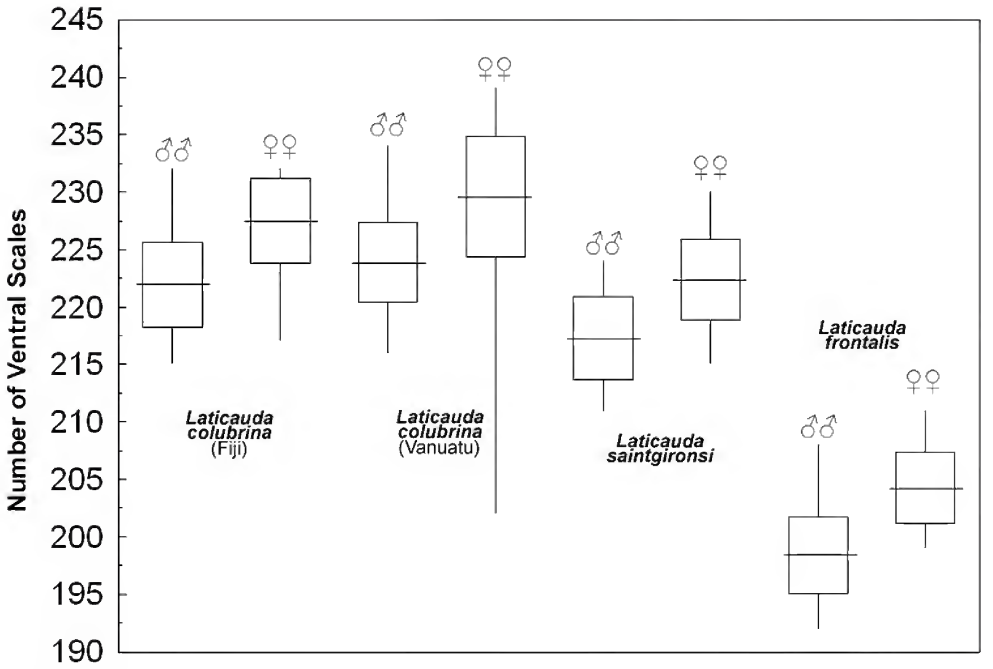

Fig. 8. Geographic and sexual variation in ventral scale numbers in *Laticauda frontalis, Laticauda saintgironsi* and two regional populations of *Laticauda colubrina*. Vertical line indicates range; horizontal line represents mean; rectangle represents 2 standard deviations.

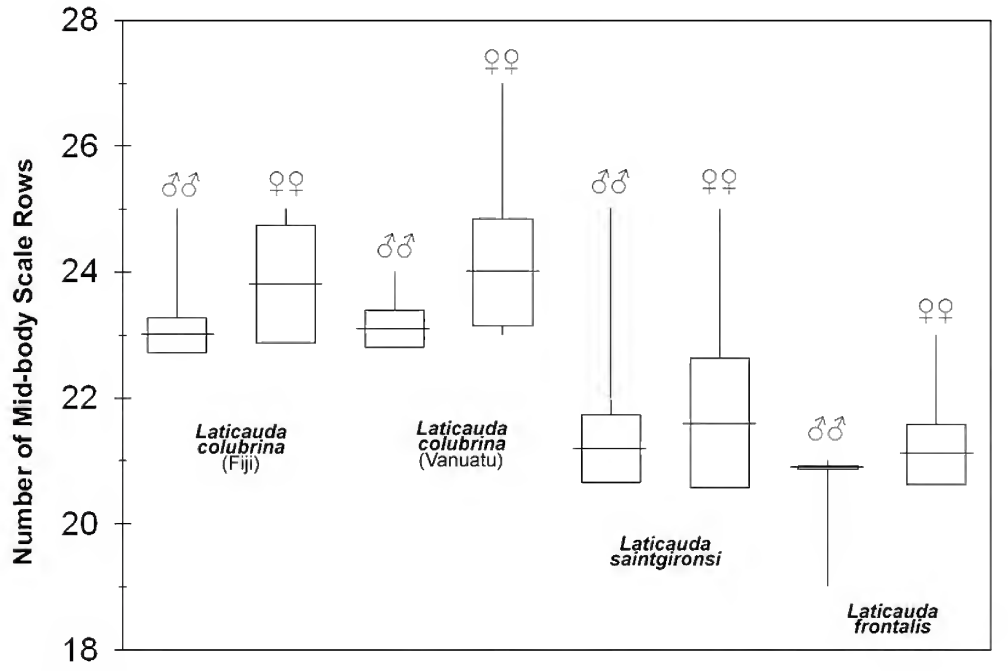

Fig. 9. Geographic and sexual variation in mid-body scale row numbers in *Laticauda frontalis, Laticauda saintgironsi* and two regional populations of *Laticauda colubrina*. Vertical line indicates range; horizontal line represents mean; rectangle represents 2 standard deviations.

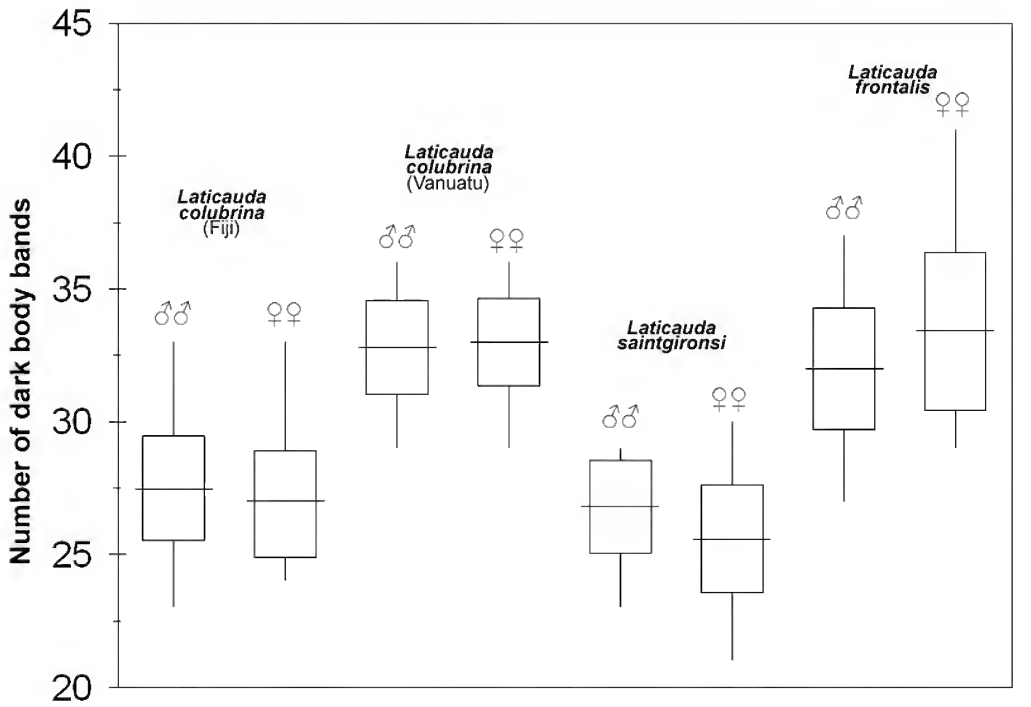

Fig. 10. Geographic and sexual variation in numbers of dark body bands in *Laticauda frontalis, Laticauda saintgironsi* and two regional populations of *Laticauda colubrina*. Vertical line indicates range; horizontal line represents mean; rectangle represents 2 standard deviations.

42 in males, 25–34 in females, Table 1). The total number of dark body bands ranges from 23–29 (males) and 21–30 (females), while the number of dark tail bands ranges from 3–4 (males) and 2–3 (females).

Distribution. Known only from the French Territory of New Caledonia, where it occurs around the entire coast of the main island (*Grande Terre*) and its many offshore islands, often in very large numbers locally. It is recorded from the Loyalty Islands, but there are no current records there of syntopy with its closest congener, *Laticauda frontalis*.

Ecology. This is a typical member of the *Laticauda colubrina* complex, spending much of its time in coastal waters feeding on a variety of eels in shallow reef waters, alternating with periods spent ashore sheltering in shoreline vegetation, piles of dense litter, or, on rocky shorelines, in crevices and caves, or under boulders. They may travel some hundreds of metres inland, and climb to the tops of rocky hills and islands that may be 100 m or more in elevation. Aggregations of 30 or more individuals are often encountered in single refuges, while some hundreds of individuals may be found on individual small islands within the lagoons of large reef systems.

An extensive summary of the distribution and ecology of this species, under the name *Laticauda colubrina*, has recently been provided by Ineich & LaBoute (2002). Other studies, also as *L. colubrina*, include St Girons (1964), McCarthy (1986) and Shine *et al.* (2003). The species is abundant and wide-ranging around the coast of New Caledonia and its numerous off-shore islands.

Etymology. This species in named for the late Dr Hubert Saint Girons, whose many outstanding contributions to international herpetology ranged across disciplines and continents. In order for future workers to clearly identify the patronym, the name *saintgironsi* is formed directly from the modern personal name as a noun in the genitive case.

Discussion

The discovery that *Laticauda frontalis* is a dwarf species living sympatrically and syntopically with *Laticauda colubrina* in Vanuatu, the two morphologically almost indistinguishable and exploiting and competing for the same aquatic and terrestrial microhabitats and food resources, raises two obvious questions: how do these species maintain their ecological integrity without one displacing the other? and how did this situation evolve in the first place?

Published morphological and molecular genetic data (e.g., McCarthy, 1986) indicate that living laticaudine species, especially *Laticauda colubrina s.l.*, display significant regional variation but with a level of overlap that makes recognition of separate taxa difficult and ambiguous. Until further molecular data are available that might help to answer these questions, only tentative explanations can be offered.

The available data suggest that *L. frontalis* and *L. saintgironsi* are sister species representing a distinct lineage within the *colubrina* complex, bringing the total number of recognized species in this complex to four (with *colubrina* and *guineai*). The former species-pair share a small suite of

characters in common, though these characters are largely expressed through modal values: low variability in body scale rows numbers, lower ventral scale counts, lower subcaudal counts, and lower body band numbers (Table 1, Figs. 8–10). These differences are also reflected in other measures of body form. *Laticauda saintgironsi* and *L. frontalis* share similar regression curves, by sex, for snout-vent length *vs.* tail length (Figs. 6–7) and snout-vent length *vs* live weight (Figs. 4–5) when compared with curves for sympatric or adjacent populations of *L. colubrina*.

Research on the venom chemistry of these two species indicate only minor differences in amino acid residues in laticotoxin sequences, shared by *L. frontalis* and *L. saintgironsi*, that separate both from syntopic or geographically proximate populations of *L. colubrina* from Vanuatu and Fiji (T. Tamiya, N. Tamiya, pers. comms.).

The current distribution of *Laticauda* within the southwest Pacific region appears to be the outcome of a series of speciation events involving local or regional isolation of populations of widespread taxa, followed in turn by reinvasions of the widespread parent species that, through subsequent morphological and ecological character displacement, resulted in either sympatry or mutual exclusion of closely allied congeners.

If, as we propose, the dwarf *Laticauda frontalis* represents a paedomorphic member of the *L. colubrina* complex, then it must clearly be derived from one of the larger members of the complex. Given its many shared features with the larger, non-paedomorphic *L. saintgironsi*, and their marginally overlapping geographic ranges, one likely explanation is that *frontalis* evolved in the southern part of Vanuatu where *saintgironsi* (or its endemic New Caledonian precursor) came into contact with the northern *colubrina*. Their common ecologies may well have put considerable pressure on either species to minimize ecological competition by selecting for early maturity, and its associated reduction in body size, by utilising an inherent predisposition to progenesis in this group of snakes. Current work in preparation suggests that both *Laticauda crockeri* and *Laticauda schistorhynchus* also represent localized paedomorphic species derived from once geographically-isolated outliers of more widespread *Laticauda* species. Progenesis offers a built-in mechanism for rapid speciation, consistent with the available evidence that genetic variability in members of the *L. colubrina* complex is low and that existing differences are of relatively recent origin. We hypothesize that *Laticauda frontalis* and *Laticauda saintgironsi* represent a distinct lineage (clade) within the *Laticauda colubrina* complex.

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